Systematic Zoology

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Monophyletic Classification and Evolution

R. S. BIGELOW

PERHAPS the majority of contemporary taxonomists strive toward the "theoretical ideal" of a monophyletic classification. It is therefore advisable to consider: (1) what is meant by the term "monophyletic," and (2) whether or not such a classification is theoretically justifiable on evolutionary grounds.

Mayr (1942) says: "We employ the term monophyletic as meaning descendants of a single interbreeding group of populations, in other words, descendants of a single species."

Simpson (1953) says: "In evolutionary classification it is an expressed ideal that all recognized and named groups should be monophyletic, presumably that each should be theoretically traceable to a single species at its beginning." He adds that: "In a practical way, the ideal of monophyletic classification is adequately approached if all lineages leading into a given higher category arose from one ancestral group of lower categorical rank." (Monophyletic classification is clearly referred to as an ideal which should be at least "adequately" approached.)

Although it is not stated in these definitions, monophyletic classification obviously involves more than mere origin from a single species. If all organisms share a common ancestry, then *any* group is descended from a single species. Unless the time element is introduced, say, as follows: "the members of a monophyletic group share a *more recent* common ancestry with one another than with any member of any other such group of equal categorical rank," the term "monophyletic" is meaningless. The time element is the very essence of monophyletic classification.

If all species had always been evolving differences from one another at the same rate, then recency of common ancestry would correspond with overall similarity and difference. There is ample evidence, however, that rates of evolutionary change have varied and fluctuated both within and between evolving phyletic lines. In the course of time these different, fluctuating rates of change must have produced complex overall differences that do not correspond with recency of common ancestry. It is not safe, therefore, to assume that the extent of overall similarity between contemporaries corresponds with the relative recency of their common ancestry. Even in fossil series, ancestral continuity is more likely to be recognized between successive representatives of those phyletic lines that were evolving more slowly (retaining greater similarity to one another), and less likely to be recognized between successive representatives of phyletic lines that were evolving more rapidly (retaining less similarity to one another). Where overall similarity corresponds least with recency of common ancestry, the lack of correspondence is least likely to be detected. Despite these difficulties it has been possible to detect many cases in which overall similarity does *not* correspond with recency of common ancestry (Simpson, 1945). Clearly, overall similarity and recency of common ancestry are two separate and distinct phenomena which must be considered separately, not as though one is automatically given by the other. Classification must be based on one or the other, not on both, if philosophical confusion is to be avoided.

Two species may be very similar and yet, if their ancestors evolved slowly, their *common ancestors* may be very remote in

time. The phyletic lines leading directly from the common ancestral species to these two descendant species may also have produced other species which evolved more rapidly. In terms of recency of common ancestry, the two similar species may each be more closely related to many very different species than they are to one another. For example, certain reptiles may be more closely related to birds, or to mammals, than they are to one another. Crocodiles are regarded as more closely related to birds than to lizards or turtles. The monophyletic ideal demands that the overall similarity between these "distantly related" species, as well as the extensive overall differences between them and those species with whom they share a more recent common ancestry, should be disregarded. Overall similarities and differences are usually *not* disregarded in such cases, however. Crocodiles are classified with other reptiles, not with birds. It is monophyletic classification that is disregarded in such cases. Where the ideal of monophyletic classification is clearly attainable it is rejected in favor of overall similarity. Monophyletic classification, therefore, is obviously not the ideal of taxonomy, and to state that it is tends to confuse the philosophical basis upon which the science of taxonomy rests. The mere contradiction of such statements (e.g. by placing crocodiles closer to lizards than to birds) will not eliminate this confusion.

Without overlooking the fact that *resemblance reflects phylogeny,* it is well to bear in mind that *difference reflects evolution,* and that the nature and extent of these similarities and differences, not the times during which they have been retained or effected, is the primary concern of evolutionary classification. Organisms whose ancestors evolved very little relative to one another should not be separated merely because evolution has been slow, or grouped with organisms with whom they share a more recent common ancestry despite extensive overall differences that have evolved between them. Evolution is change, not time. If classification is to correspond with evolution, it must be based on the extent of overall difference, not on time. Monophyletic classification is based on *recency* of common ancestry (i.e. on time), and therefore should not be regarded as even a "theoretical" ideal.

If monophyletic classification is not the ideal of taxonomy, the fact should be clearly recognized. When terms such as "closely related" and "phylogenetic affinity" are applied to organisms whose ancestry is unknown, they should *clearly* refer only to overall similarity and should not imply that this automatically corresponds with recency of common ancestry.

REFERENCES

MAYR, E. 1942. Systematics and the origin of species. Columbia Univ. Press, New York.

SIMPSON, G. G. 1945. The principles of classification and a classification of the mammals. *Bull. Amer. Mus. Nat. Hist., 85*:i-xvi, 1–350.

SIMPSON, G. G. 1953. The major features of evolution. Columbia Univ. Press, New York.

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A Study of Methods of Color Determination

DARL E. BOWERS

IN THE course of an investigation of correlations of color of wren-tits (*Chamaea fasciata*) with environmental gradients, the author found it necessary accurately to designate and record the colors in question. Although my investigation was not taxonomically oriented, the description and evaluation of the methods of color determination here presented may be useful in taxonomic studies wherever colors are to be considered.

North of San Francisco Bay, California, there are three races of *Chamaea fasciata.* The darkest birds, ascribable to the race *C. f. rufula,* exist in the coastal humid belt from San Francisco Bay northward. The lightest birds, of the race *C. f. henshawi,* occur interiorly from the southern tip of the Vaca Mountains northward and northwestward. In between these two, the appropriately named race *C. f. intermedia* is found.

The color of the breast and belly regions of these birds shows a gradation from "moderate brown" through various color steps to a lighter, buffier, "pale yellowish-brown." The problem of color definition is evident from the adjectival terms used here to describe these extremes in breast color. The terms "moderate brown" and "pale yellowish-brown" have meaning to the author in connection with the birds studied because of experience with them. But how similar would these colors appear in the mind's eye of a reader not having had such experience with these particular birds? It is my contention, in view of the high degree of variation in human color-vision response and experience, that color designation in adjectival terms is not sufficiently reliable to convey to others the color sensations perceived by a worker. Because of this belief, I have gone to some lengths to find objective methods of designating the colors of the birds in question.

A very important reference for the description of colorimetry is a book by the Committee on Colorimetry of the Optical Society of America (1953). This work is valuable not only for its excellent treatment of the concepts of color and color vision, but for its extensive bibliography in the fields of color and colorimetry.

Visual Methods

The most common method of labelling a color is to give it the name of a color chip in some standard color atlas which the sample color most closely approximates. The color reference used most for biological and especially ornithological work has been that of Ridgway (1912). While it is an important contribution, it has several shortcomings. Among its faults are the designation of colors in adjectival terms, the unequal visual steps between color chips, and the use of pigments that are not permanent. Concerning this last point, Ridgway himself expected his guide to be superseded in a few years by better ones. With age, some of these pigments have changed hue and some have loosened and have flaked off the paper (see Illman and Hamly, 1948, and Hamly, 1949, concerning the fading of the Ridgway colors).

Villalobos-Dominguez and Villalobos (1947) have published an atlas of colors which has gained some users among ornithologists. Its main disadvantages are these: it is printed, and unfortunately printing inks can never reproduce the intensity of color possible in paints; the paper on which it is printed has a glossy

surface which produces highlights and which does not approach plumage texture as closely as painted colors; the color swatches are too small for adequate retinal stimulation ($\frac{3}{8} \times \frac{3}{8}$ inches); the color swatches are interrupted by a $\frac{1}{8}$-inch hole punched in each with the aim of serving as windows through which objects to be tested are scanned—a procedure that introduces distortion, since it is important to compare areas of equal size and shape that are illuminated in the same way; the system is basically inconsistent in that there are not equal color steps between colors designated with the same indices (equal steps are important in interpolation between color chips); the printing is on paper that is not truly white and the "black" of the printing ink is not truly black; the system has no equivalence or comparative relationship with other color systems.

Other systems and sets of color charts have been prepared by other workers; many of these are intended for specific uses, as in horticulture, the textile industry, paint manufacture, and interior decoration. Among these is the Ostwald system used widely in Europe.

Maerz and Paul (1951) have published a color dictionary using over 7000 colors. Keyed to about 4000 of these are color names that have gained recognized meanings. Some workers in ornithology have used this book to advantage over that of Ridgway. The Maerz and Paul dictionary is printed on glossy paper which offers some difficulty because of surface reflections, and as mentioned previously, it is not possible to achieve as high a saturation of color in printing as it is in pigment-painted samples. Therefore, some of the purest colors cannot be represented by Maerz and Paul. Many of the rich browns found in birds are likewise not shown. It has been used in the present study to compare its designations with those of other systems. Up to now the spectrophotometric data on this book have not appeared, but when this information is available, the Maerz and Paul colors will be describable directly in the tristimulus notation (numerical designations of colors) of the International Commission on Illumination and therefore will have objective and universal meanings. This latter method of color designation will be discussed later with regard to spectrophotometric systems.

In the system of Maerz and Paul, the basic problem still exists of relying mainly on adjectival terms for color designation, although in this work these terms do have fairly reproduceable meanings. The authors note in the preface to the first edition (1942) that "we were concerned only with standardization as applied to color names and the color sensations on which the names are bestowed. We were not concerned with those systems that refer to colors by numerical terms either as regards the special forms of such numerical terminology or the methods by which the colors were arranged. Today, we are fortunate in having the magnificent 'Munsell Book of Color' (standard edition 1929), which in correctness of principle, completeness of treatment, and artistic beauty of presentation provides a technical classification of high standing in the field of color."

The Munsell system is an arrangement of colors in a three-dimensional Euclidean solid, each point in which represents a distinct color designated by three coordinates. It was devised and in use in 1905 before the Ridgway color guide was published and yet surprisingly it has been overlooked or rejected by biologists. Ridgway knew of the Munsell system and referred to it in a footnote in which he mentioned his preference for the term "tone" over that of "value" used by Munsell to designate lightness or darkness. The Munsell arrangement is the adopted color system of the United States National Bureau of Standards for use in the naming of colors and the grading of such agricultural products as cotton, hay, and natural pharmaceuticals. Much research has been done to define more accurately the colors that were originally published and to in-

crease the usefulness of the standard colored papers available from the Munsell Color Company, Inc. For a discussion of the Munsell color system, the reader is referred to a paper by Nickerson (1946), or to any recent edition of the Munsell booklet, or to an excellent article entitled "Color" in *Life* magazine (July 3, 1944). Actually, not all colors have been published by the Munsell Company, but the basic plan provides a point in the color solid for any possible pigment color. Publication of all colors is not feasible, but interpolation between those represented is possible since the colors of the standard patches are equally spaced visually. Degrees in any direction between color chips may be judged and numbered accordingly by decimal notation.

I think the Munsell color system is the best arrangement of colors available. The published colors are flat pigments painted on mat surfaces. The greatest disadvantage of the Munsell color guide lies in the fact that it does not contain as many color samples as are desirable for this method of color determination although it has nearly as many as the Ridgway atlas. Interpolation is feasible but requires practice and adds more of the subjective element. Of course many structural colors as formed in many birds cannot be duplicated with either printing inks or paint pigments and this represents a limitation to the use of any color dictionary or standard papers. However, the Munsell system used in conjunction with disk colorimetry provides one of the best methods of visual color determination.

Disk colorimetry is a more refined method of using standard colored papers than those discussed previously. Color determination is here again one of visual comparison between sample and standard, but an important advantage lies in the fact that the standards are more flexible than those presented in book form and hence allow greater accuracy of interpolation between the reference papers. The equipment for this work consists of a motor-driven backing disk which supports several colored papers. These Maxwellian disks, cut from the standard papers, slit to interleave and representing hues to either side of a sample color together with a relatively white and a relatively black paper, are applied to the backing disk. The spinning of these causes the colors to fuse into a single color in the eye. The percentages of the four papers that show can be measured with a protractor or by using a backing disk scribed in decimal divisions, and these values are used to calculate the tristimulus coordinates (see p. 182) of the color that is represented when these four colors fuse in the observer's eye. Varying the relative amounts of the standards showing shifts the composite color produced until it can be made to match that of the sample under test (see Figure 1 for a simple layout). Refinements of this method are discussed by Nickerson (1946).

Any colored papers may be used provided the tristimulus values are known for them. The simple spinning disk method has been used in the present study with Munsell standard papers obtained from the Munsell Color Company, Inc., Baltimore, Maryland. The color notations of the standard disks used are as follows:

TABLE I—COLOR NOTATIONS OF STANDARD DISKS USED.

			INTERNATIONAL COMMISSION ON ILLUMINATION TRISTIMULUS VALUES FOR ILLUMINANT "C" (DAYLIGHT)		
	HUE	VALUE/CHROMA	*X*	*Y*	*Z*
"Red"	5 YR	4/8	.1676	.1414	.0499
"Yellow"	5 Y	6/8	.2839	.2965	.0623
"Black"	Neutral	2/	.0294	.0302	.0341
"White"	Neutral	9/	.7119	.7286	.8527

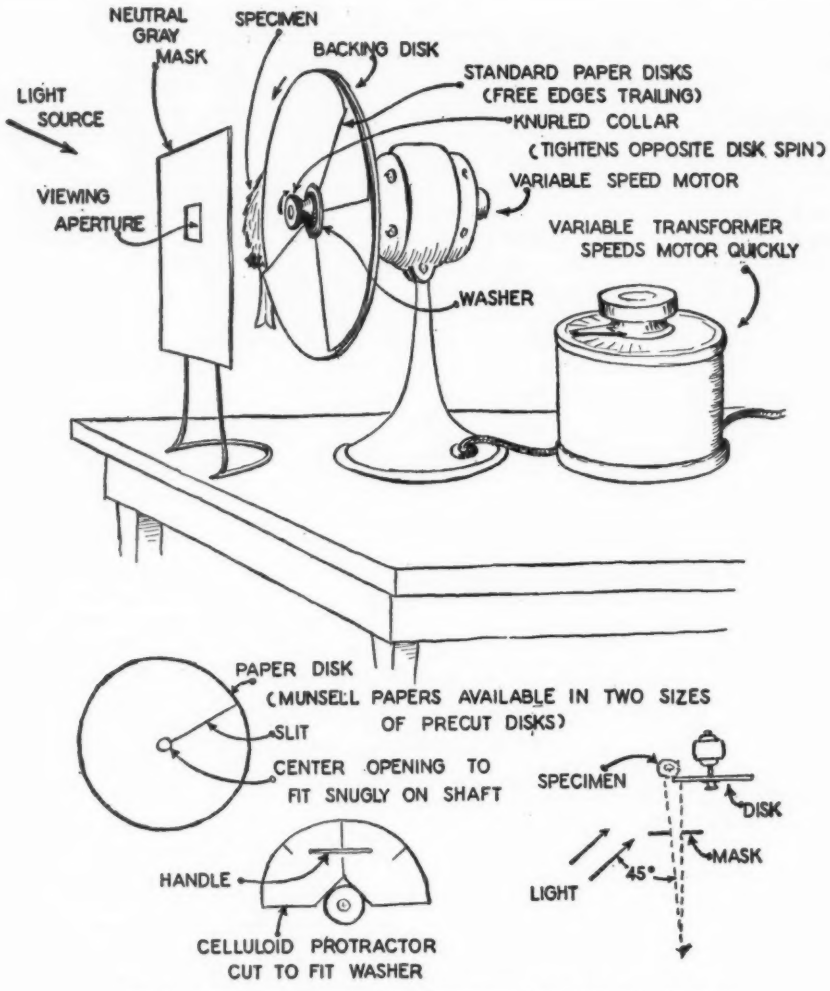

FIG. 1. Arrangement of the elements used for disk colorimetry.

These colors were chosen because they bound a wedge-shaped segment of the Munsell color solid within which fall all the breast colors of the wren-tits as ascertained by comparison with the Munsell color guide. Various mixtures of the four papers will produce the multitude of colors that lie between these extremes.

A neutral (hue-less) gray mask (Munsell value 5/) was supported vertically in front of the spinning disk. A $\frac{7}{8} \times \frac{7}{8}$-inch window was cut near the center of the mask. The spinning disk was viewed through half of the window in the mask and the bird specimen, held just behind the disk, was viewed through the other half of the window. Contiguous areas were in this way viewed through the one opening. Both disk and specimen were placed six to eight inches behind the

mask. This allowed north sky light to strike the colored surfaces at about 45 degrees from the normal, without causing a shadow from the mask, and to be reflected to the observer through the mask window perpendicularly to the surfaces. The observer sat low and to one side of the window facing away from it. The position of the colored surfaces behind the mask allowed the observer to focus his eyes on the mask and thus purposely throw out of focus the test areas. Since the birds are not uniformly colored, this had the effect of blurring the streakings on the breast and of causing a more uniform color to appear. The disk was alternately spun and rearranged until the closest match was obtained between disk and specimen. See the appendix for a sample calculation of the resulting color coordinates. The method of calculation of the tristimulus values x, y, and z is that of Nickerson (1946).

Precautions. Apart from the selection of a good color standard there are certain general precautions that must be heeded in making visual comparisons. First and most important is the selection of the kind of light source in which the comparisons are to be made. The most common and least expensive is that of normal daylight, the light reflected from a cloudless, blue, north sky with no direct sunlight. The quality of such light is fairly uniform, but the caprices of weather or the presence of smog or nearby reflecting objects may appreciably affect its quality and hence change visual color judgments.

There are artificial sources of illumination that are standardized and available to workers in colorimetry. Of these, illuminant *C* of the International Commission on Illumination is the closest approximation to normal daylight. This light source can be used in an otherwise darkened room in any weather or at any time of day and has thus the value of constancy that natural daylight lacks. There are other accepted standard illuminants that can be used. The important point is that whatever the illumination used in color determinations, it must be specified in the interests of reproducibility of color matches. Color comparisons in the present study were made before a large window in a cloud-free north light.

Light should impinge on the sample and the standard at about 45 degrees from the surfaces; viewing should be done perpendicularly to the surfaces. Colors reflected at this 45-degree angle represent more nearly their actual makeup than at other angles. Needless to say the light should strike both sample and standard as similarly as possible.

Comparison of sample and standard should be made viewing each through the same sized windows in neutral gray masks. This helps focus attention on a single color block at a time and removes the effect of surrounding colors, which may be considerable. The importance of a mask of neutral "color" is undoubtedly obvious, but the importance of a proper color value of the mask is less well known. If a circle of gray is surrounded with a lighter gray, and another circle of the same value of gray as the first circle is surrounded similarly with a darker gray, the circle in the first instance appears much darker than the circle in the second instance. The surrounding lighter gray has induced darkness in the circle while the surrounding darker gray has induced lightness in the circle. For a clear demonstration of this, see the article in *Life* mentioned earlier. For extreme accuracy in color work a series of masks should be used, each of the proper value for the colors to be tested. Next best is a mask of medium value gray or a black. In the interests of reproducibility of determination, the kind of a mask that has been used should be stated.

In the present study, masks of near-neutral black velour paper were used for comparisons with color books. Three windows cut in the mask were utilized for work with the color books, as in the method described by Judd and Kelly (1939). The sample bird was placed under the middle window, flanked by the

constant hue pages of the *Munsell Book of Color* (pocket ed. 1929, 1942) representing those standards between which the sample fell. Determinations of value were made next, then those of chroma (saturation or intensity). Interpolation was necessary between the standard colors. The same colored masks and north light were used in comparing the wren-tits with the Ridgway and Maerz and Paul color guides.

With regard to the degree of color discrimination, the Committee on Colorimetry (1953, p. 126) remarks that "even in the simplest situations, . . . there are at least twenty different factors affecting the fineness of the discrimination." The reader is referred to this source for descriptions of these and factors additional to those discussed that are important in color determinations; also this reference discusses several types of colorimeters.

Machine Determinations

Use was made of a General Electric-Hardy recording spectrophotometer, which is a special kind of colorimeter, available in the illumination laboratory of the College of Engineering at the University of California in Berkeley. This apparatus compares the reflectance of light from a sample to be tested with the reflectance of this light from a standard magnesium oxide block and records graphically the proportions of the various wave lengths reflected by the unknown. The resulting curve represents the percentages of energy reflected from the sample throughout the visible spectrum. Mathematical manipulation of the ordinates of such a graph by the weighted ordinate method or the selected ordinate method as outlined by Bouma (1947), the Committee on Colorimetry (1953), or Hardy (1936) gives three numerical values which describe the color that is represented by such a curve. These numbers, the tristimulus notation of the International Commission on Illumination, express the relative amounts of three imaginary but mathematically defined monochromatic lights, a red, a green, and a blue, respectively, which when blended match a given sample color under a given illumination for an average normal human eye. This imaginary "standard observer" of the I.C.I.[1] is also mathematically defined and corresponds to the vision possessed by over 90 per cent of the population. (See a paper by Judd, 1933, for a more complete description of the standard observer and the coordinate system for colorimetry.) The tristimulus notation is expressed as absolute values X, Y, and Z, or as fractional values, x, y, and z where $x+y+z=1$. The Y value in addition to representing green gives directly the luminous intensity of the sample and represents the total per cent of reflectance of all the light relative to that from a magnesium oxide block. The x and y coordinates, which adequately label a color under a given illuminant, do not tell much about the physiological stimulation such a color produces in the human visual apparatus. They can be used with an I.C.I. chromaticity diagram, however, to give psycho-physical descriptions of the colors in terms of dominant wave length (hue), brightness (value), and purity (chroma). Chromaticity diagrams are available in several of the references cited, but those presented by Hardy (1936) are especially useful because of their relatively large size. Such designations can also be converted into the Munsell notation of hue, value, and chroma by use of charts prepared for this purpose and published by Newhall, Nickerson, and Judd (1943), or Nickerson (1946). Using the Judd and Kelly charts (1939) for Munsell color areas, these same coordinates can be expressed in adjectival terms.

With such a machine as the recording spectrophotometer, the Munsell standard papers themselves have been evaluated. These comparisons between the Munsell system and spectrophotometric recordings

[1] Sometimes abbreviated C.I.E. for the French "Commission Internationale de l'Eclairage."

have afforded precise color designations of the highest order yet devised. There is thus a unique inter-conversion possible between readings of machine-scanned samples and those of visually compared samples. Actually, although there is individual variation in human color vision, man's discrimination is superior to that of the best available photoelectric machines. The variable presentation of the sample to the machine appears to be a source of appreciable deviation in readings, especially with birds in which all feathers to be tested and indeed even all parts of each feather are not the same color.

Since the spectrophotometer readings serve as an objective check on determinations made in other ways, several arrays of wren-tit specimens were tested with the spectrophotometer in the illumination laboratory. These represent the gamut of color expression of the breast area for the birds collected.

Nine specimens representing a fairly evenly graded seriation of breast coloration were selected from recently collected birds in fall plumage. The lightest bird was labelled "1" and the darkest "9." These nine specimens were then analyzed by the various methods just described. The results of these color measurements are best shown in tabular and graphic form.

The Ridgway guide was used as a point of departure. The colors indicated by this book for the series of nine birds are shown in Table II. Munsell notations for the Ridgway colors are available in a paper by Hamly (1949), and those pertaining to the colors used here are also given in Table II. Hues are expressed by numerical designations and the initials of that hue (YR=yellow-red); value follows with a numerical notation before the diagonal bar; chroma is indicated by numbers after the diagonal.

The Munsell hues shown by these data fairly well agree with other information to the effect that the darker birds are more reddish, a trend shown by the movement from 10 YR to 5 YR. Bird number 1, however, appears exceptionally out of line with regard to hue which is very likely due to a difference between the book used here and the copies utilized by Hamly for his Munsell notation. The value figures show increasing darkness from bird 1 to bird 9 (complete black is 0.0/, white is 10.0/) while chroma shows very little change (saturation runs from /0.0 at neutrality to /14.0 or more in certain hues). Note that the adjectival terms do not offer much aid in analyzing the changes that occur in the three dimensions of the colors.

The results of the comparison with the dictionary of Maerz and Paul are shown in Table III. The Munsell notation for 20 of the 57 Maerz and Paul dictionary plates were published by Nickerson (1947). In Table III will also be found the Munsell

TABLE II—RIDGWAY COLOR NUMBERS AND NAMES FOR NINE BIRDS WITH MUNSELL NOTATION EQUIVALENTS FOR THESE COLORS.

BIRD	RIDGWAY COLOR NUMBER	NAME	MUNSELL EQUIVALENTS
1	17‴ O-Yd	Vinaceous-buff	6.5 YR 8.0/3.0
2	17‴ O-Yb	Avellaneous	10 YR 7.0/3.0
3	17‴ O-Yb	Avellaneous	10 YR 7.0/3.0
4	17‴ O-Yb to 17‴ O-Y	Avellaneous to wood brown	10 YR 7.0/3.0 to 9 YR 6.0/3.0
5	17‴ O-Y	Wood brown	9 YR 6.0/3.0
6	17‴ O-Y	Wood brown	9 YR 6.0/3.0
7	17‴ O-Y	Wood brown	9 YR 6.0/3.0
8	17‴ O-Y to 13‴ OY-Oi	Wood brown to army brown	9 YR 6.0/3.0 to 5 YR 4.4/2.5
9	13‴ OY-Oi	Army brown	5 YR 4.4/2.5

Vinaceous-buff is the "lightest" color and army brown the "darkest."

TABLE III—MAERZ AND PAUL COLOR NUMBERS AND NAMES FOR NINE BIRDS WITH MUNSELL NOTATION EQUIVALENTS FOR THESE COLORS.

BIRD	PAGE-COLUMN-ROW	NAME	MUNSELL EQUIVALENTS
1	13-B-5	Mavis, Grain, Pecan	10 YR 6.0/2.3
2	13-B-6	Almond bisquit, Pawnee, Doe	8 YR 5.8/3.0
3	13-B-6	Almond bisquit, Pawnee, Doe	8 YR 5.8/3.0
4	13-B-6	Almond bisquit, Pawnee, Doe	8 YR 5.8/3.0
5	14-B-6	Camel's hair, Bobolink, Deer	10 YR 5.0/2.0
6	14-B-6	Camel's hair, Bobolink, Deer	10 YR 5.0/2.0
7	14-D-7	Adobe	10 YR 5.0/3.1
8	14-C-8	Mocha bisque	7 YR 4.5/4.0
9	15-A-11 to 15-C-11	Cocoa to Cocoa brown	5 YR 3.5/3.5 to 7 YR 3.7/2.5

notation taken from this paper for the Maerz and Paul colors used here. It will be noted that several synonyms are listed for most of these colors, as would be expected from a dictionary. Again, the adjectival terms allow little analysis of the differences.

The only consistent trend in these data is in value. Bird 1 is lightest in value and the others become darker stepwise to number 9 which is the darkest. Hue shows a variable trend toward redness in the darker birds and there is faint indication of increase in chroma toward the dark end of the scale.

Two comparisons of the nine selected birds with the *Munsell Book of Color* (pocket ed. 1929, 1942) gave the results listed in Table IV. The averages from two determinations of each of the three dimensions of these colors are plotted in Figure 2. A general overall trend toward redness in the darker birds is shown by this figure. Likewise a general lowering of value appears toward the darker birds. There is a slight correlated trend evident in chroma toward higher purity of color.

Judd and Kelly (1939) have published a system of adjectival color names for various areas and volumes of the Munsell color solid. These represent the standards of the Inter-Society Color Council and the National Bureau of Standards for these portions of the color solid. The equivalent

TABLE IV—MUNSELL COLOR NOTATION OBTAINED BY DIRECT COMPARISON OF NINE BIRDS WITH THE *Munsell Book of Color;* EQUIVALENT ADJECTIVAL TERMS OF JUDD AND KELLY.

BIRD	HUE VALUE/CHROMA	JUDD AND KELLY NAMES
1	10.0 YR 6.0/3.0	Pale brown—light yellowish brown—moderate yellowish brown
	10.0 YR 6.5/3.0	Very pale brown—pale brown—light yellowish brown—weak yellowish orange
2	9.0 YR 5.5/3.0	Pale brown—moderate yellowish brown
	9.0 YR 6.0/4.0	Light yellowish brown
3	10.0 YR 6.0/3.0	Pale brown—light yellowish brown—moderate yellowish brown
	10.0 YR 5.8/4.0	Light yellowish brown
4	9.0 YR 5.0/3.0	Pale brown—weak brown—moderate yellowish brown
	10.0 YR 5.5/4.0	Light yellowish brown—moderate yellowish brown
5	9.0 YR 5.5/3.0	Pale brown—moderate yellowish brown
	7.8 YR 5.3/5.0	Light brown—moderate yellowish brown
6	8.5 YR 5.0/2.5	Pale brown—weak brown
	7.5 YR 5.3/5.0	Light brown—moderate yellowish brown
7	9.0 YR 5.0/3.0	Pale brown—weak brown—moderate yellowish brown
	7.5 YR 4.9/5.0	Moderate brown—moderate yellowish brown
8	8.5 YR 4.5/2.5	Weak brown
	6.8 YR 4.3/4.5	Moderate brown—moderate yellowish brown
9	8.0 YR 4.5/3.0	Weak brown—moderate brown
	5.5 YR 4.0/4.0	Moderate brown

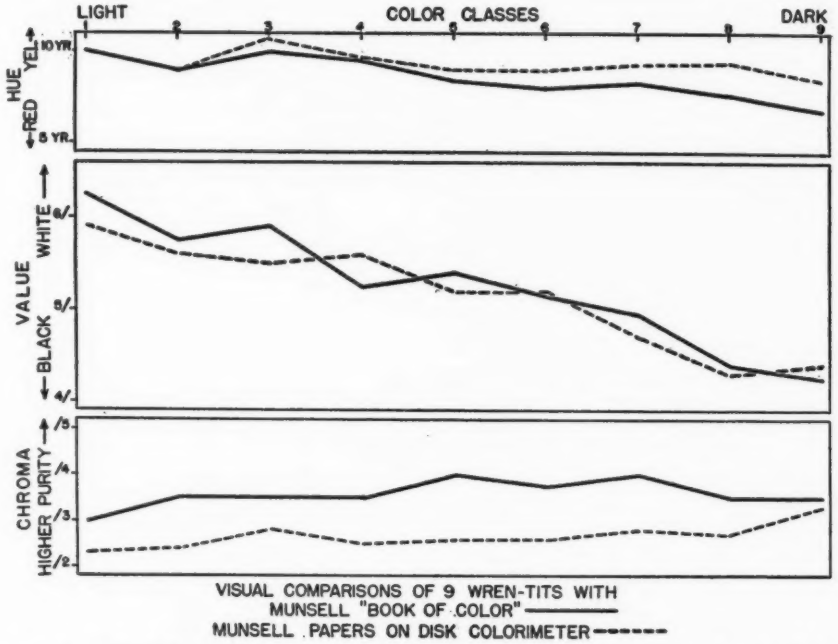

FIG. 2. Graphs of the three dimensions of color in Munsell designations for the breast plumage of nine birds representing the gamut of color expression.

terms of Judd and Kelly for the Munsell notations gained from the direct comparison of the wren-tits with the *Book of Color* are given in Table IV. The double and triple terms indicated for all but one of the nine birds indicate that these colors occur at the boundaries between color volumes and thus must all be mentioned. This list of names stresses further the lack of absolute meaning inherent in adjectival terms, no matter what their source, for refined color determinations.

The same nine wren-tits were analyzed by comparison with the disk colorimeter using the four Munsell standard papers described earlier. The findings are reported in Table V and Figure 2.

The same trends are evident in hue and

TABLE V—TRISTIMULUS VALUES AND EQUIVALENT MUNSELL TERMS FOR NINE BIRDS OBTAINED BY USE OF THE DISK COLORIMETER WITH MUNSELL STANDARD PAPERS.

BIRD	TRISTIMULUS VALUES (*z* NOT NEEDED)		BRIGHTNESS PER CENT	MUNSELL NOTATIONS
	x	*y*	Y	
1	.356	.352	29.2	10.0 YR 5.9/2.3
2	.360	.353	25.7	9.0 YR 5.6/2.4
3	.369	.364	24.1	0.7 Y 5.5/2.8
4	.363	.356	25.4	9.7 YR 5.6/2.5
5	.367	.357	21.7	9.0 YR 5.2/2.6
6	.367	.358	21.7	9.0 YR 5.2/2.6
7	.379	.366	16.8	9.3 YR 4.7/2.8
8	.384	.369	13.7	9.4 YR 4.3/2.7
9	.397	.373	15.1	8.4 YR 4.4/3.3

value that were shown by direct comparison with the Munsell color guide. Chroma shows more of a gradient in which there is more saturation in the darker birds.

The spectrophotometric data from the same nine specimens is presented in Table VI. Seven other specimens matching the original birds 2 to 8 (numbered 2′ to 8′) were also analyzed with this machine. Two and three runs were made on some of the specimens as indicated.

Some of the original curves drawn by the spectrophotometer are reproduced in Figure 3 using an expanded vertical scale. It can be seen from these curves that reflectance per cent is higher for the longer wave lengths, the red end of the spectrum. It can also be observed that the lightest bird reflects the most light at all wave lengths while the darkest bird reflects the least for almost all wave lengths. The intermediate birds fall somewhere in between the two extremes. The curves are only roughly parallel which indicates a slight difference in the proportion of various wavelengths reflected from the different birds. The same bird did not produce perfectly identical curves for each run; however, these variations were due in the main to different feather arrangements of the birds when they were placed in the spectrophotometer. As can be seen in Table VII, which lists psycho-physical designations and Munsell equivalents, the variations in color notation between different readings from the same bird are not large. The values for the two dimensions of color (dominant wave length and purity) presented in Table VII were derived from the tristimulus quantities listed in Table VI by use of a chromaticity diagram of the International Commission on Illumination which was mentioned

TABLE VI—TRISTIMULUS VALUES OBTAINED FROM THE SPECTROPHOTOMETER FOR NINE GROUPS OF MEASUREMENTS.

BIRD	TRISTIMULUS VALUES (z NOT NEEDED) x	y	BRIGHTNESS PERCENT Y
1	.334	.335	27.8
	.332	.334	27.3
2	.334	.334	24.9
	.334	.336	25.7
	.334	.336	25.6
2′	.335	.335	24.6
3	.335	.336	23.6
3′	.339	.339	25.1
4	.338	.338	24.1
	.341	.337	27.4
	.337	.338	26.8
4′	.335	.335	23.9
5	.332	.332	22.8
5′	.335	.335	23.8
6	.334	.333	20.3
	.337	.338	23.2
6′	.334	.333	21.6
7	.340	.336	20.0
7′	.339	.337	21.1
8	.341	.335	19.2
	.345	.339	20.6
8′	.339	.337	21.1
9	.340	.334	18.7
	.343	.336	18.8

TABLE VII—PSYCHO-PHYSICAL DESIGNATIONS AND MUNSELL EQUIVALENTS FOR THE SPECTROPHOTOMETRIC DATA PRESENTED IN TABLE VI

(SPECTROPHOTOMETRIC DATA)

BIRD	DOMINANT WAVE LENGTH IN MILLIMICRONS	PURITY PER CENT	MUNSELL EQUIVALENTS
1	581	11.4	10.0 YR 5.8/1.1
	581	10.6	1.0 Y 5.8/1.0
2	582	11.1	9.0 YR 5.5/1.1
	580	11.6	1.0 Y 5.6/1.0
	580	11.6	1.0 Y 5.6/1.0
2′	582	11.7	10.0 YR 5.5/1.1
3	581	11.9	10.0 YR 5.4/1.0
3′	581	13.8	10.0 YR 5.6/1.2
4	581	13.2	10.0 YR 5.5/1.2
	583	13.8	8.0 YR 5.8/1.3
	581	13.0	1.0 Y 5.7/1.2
4′	582	11.7	10.0 YR 5.4/1.0
5	582	10.1	9.0 YR 5.3/1.0
5′	582	11.7	10.0 YR 5.4/1.0
6	583	10.8	9.0 YR 5.1/1.0
	581	13.0	1.0 Y 5.4/1.1
6′	583	10.8	8.5 YR 5.2/1.0
7	583	13.3	8.0 YR 5.0/1.2
7′	583	13.3	9.0 YR 5.1/1.1
8	585	13.2	7.5 YR 4.9/1.2
	584	15.5	8.0 YR 5.1/1.4
8′	582	13.2	9.0 YR 5.1/1.1
9	585	12.7	6.0 YR 4.9/1.1
	585	14.1	6.0 YR 4.9/1.3

YR = yellow-red, Y = yellow; 1Y is close to 10 YR, 1 YR is closer to red, R.

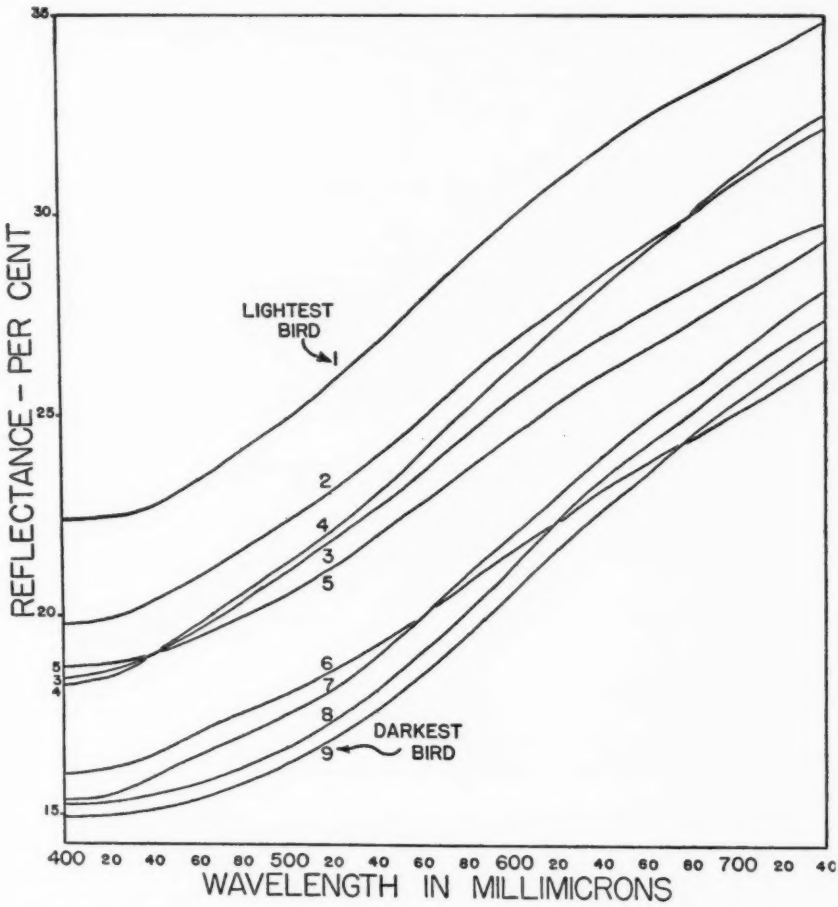

FIG. 3. Reproduction of spectrophotometric recordings with an expanded vertical scale for nine wren-tits representing the gamut of color expression.

earlier (see Hardy, 1936, or the Committee on Colorimetry, 1953, for the method of converting these data). Dominant wave length refers to hue. Brightness or *Y* (Table VI) is simply the comparison of the sum of all the wave-length reflectances with the sum of those reflectances from the magnesium oxide standard block and expressed as the per cent of the standard reflectance. Purity refers to the percentage of pure color reflected by the sample. The Munsell equivalents were derived from tables and charts in the paper by Nickerson (1946). The data of Table VII are graphed in Figure 4.

From all the data figured and tabulated, a few generalizations concerning the breast color of the wren-tits studied can now be made. There is shown an increasing amount of redness toward the darkest birds based on all the methods for hue determination. There is a slight increase in chroma or color purity, although inconsistent, toward the darkest birds.

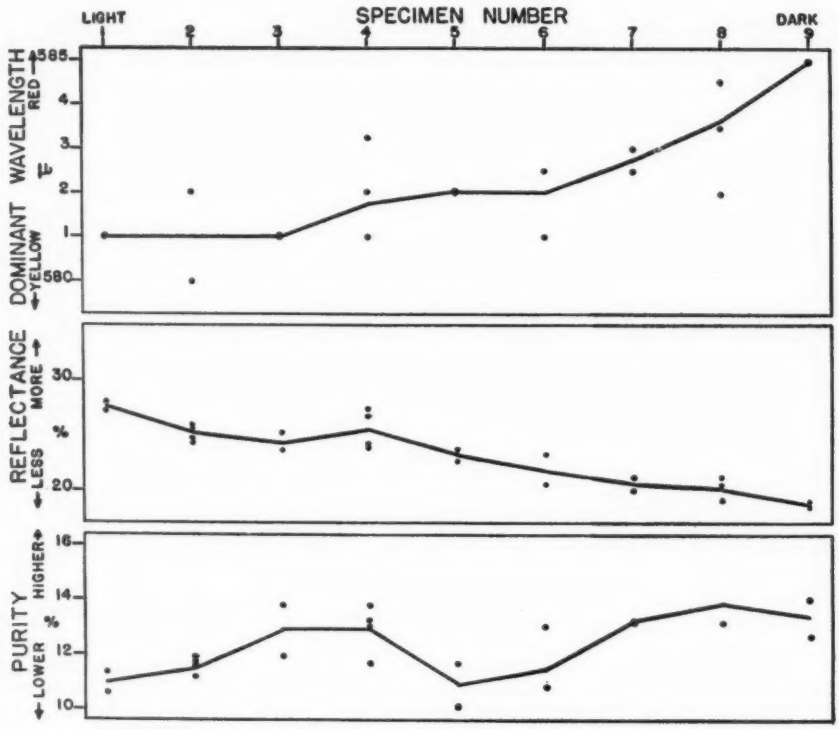

FIG. 4. Graphs of the psycho-physical terms for the three dimensions of color derived from spectrophotometric data for the nine color classes.

Specimens as Standards

The nine bird skins which were subjected to the series of color determinations were finally judged to be as reliable a set of standards for the breast colors of the specimens in hand as could be chosen. They represent the gamut of color expression, and on the basis of these analyses and simple visual judgment they form a relatively even color gradient. The description of the colors of all other specimens could in time be carried out using the methods discussed. However, it was concluded that as good an expression of the colors could be obtained by simply comparing all the specimens directly with these nine standard birds once they had been selected. The testing of the second set of seven skins in the spectrophotometer gave evidence that fairly good equivalence could be achieved by direct comparison, since this second set of specimens was chosen by visual determination with reference to the first set.

The nine standard specimens were spread on a table before a large north-facing window in cloud-free daylight. The remainder of the 275 skins, with the locality labels hidden, were then compared one by one with the breast areas of the standards and placed in the row headed by the one which was judged to be the closest match. In this way all the specimens were spread out on the table in nine rows.

Some decisions were difficult because there are three dimensions in color and not just one as this kind of separation implies. The main aspect of color on which

the decisions of position rested was that of value. Some birds that were obviously more yellowish or reddish than the standard that was closest in value were thus possibly placed out of proper position with respect to hue. Since the judgment of value is probably the most easily accomplished of the three aspects of color, it is thought that no great violence was done to the sequence of colors by this selection.

When the whole collection was spread out, slightly different viewing positions were taken and a few birds which were seemingly misplaced were rejudged with respect to the other decisions reached for that row. Some reassessments were made and better matches were thus found for those specimens in question.

The whole procedure was repeated on another day with the same physical conditions prevailing. For this second trial, 51.5 per cent of the specimens were the same as in the first trial and 95.3 per cent were judged as before or within one step, plus or minus. The effects of these differences were shown in the change in average for any given locality sample, although the greatest shift was only sixtenths of a color step.

Classifying the specimens in this way gave a code number (1 to 9) for each bird which when combined with that of the others from the same locality provided figures which can be manipulated statistically and used as indices of differences between populations from different localities. The numerical results bring out the geographic directions of the color gradient which, as originally presumed, begins with the darkest wren-tits along the coast in Marin County and runs toward lighter birds inland to northern Napa County and northwestern Yolo County where the lightest birds were found. Further discussion of this color gradient and its correlation with environmental difference is to be published elsewhere.

The colors of the dorsal plumage of the wren-tits under analysis show much less variation than those of the breast feathers. Only four color-classes could be discriminated visually; therefore, less effort was expended in defining these colors. Comparison of the back plumage with the *Munsell Book of Color* gave the following color designations: class 1 (the lightest), 2.5Y 2/2; class 2, IY 2/2, class 3, 10YR 2/2; class 4 (the darkest), 9YR 2/2. The Judd and Kelly color names for all these colors is dusky brown. Value and chroma are essentially the same in all four classes. Hue varies from a yellowish cast in the lightest class to more reddish in the darkest class. This hue sequence parallels that described for breast coloration.

I would like to acknowledge the assistance with various aspects of this color analysis of the following persons at the University of California in Berkeley: Mr. Dan M. Finch of the College of Engineering, Dr. Gordon L. Walls of the School of Optometry, Dr. Frank A. Pitelka and Dr. Alden H. Miller of the Museum of Vertebrate Zoology.

Summary

Methods for the designation of colors based on visual and machine determinations are described. One of the visual methods consists of comparing the specimens under consideration with the colors in color atlases such as those of Ridgway, Maerz and Paul, and Munsell. For objective and universal comprehension of colors, the Munsell color guide has considerable advantage over the others. In addition, the standard papers of the Munsell system can be used with a disk colorimeter, in another visual method described here, to determine colors with a finer degree of precision. Also discussed are machine determinations made with a G. E.-Hardy spectrophotometer. This is a photoelectric device not depending on human vision for its discrimination of colors. Its readings represent a check on determinations made by eye.

In order to insure a reasonable degree of accuracy and reproducibility of determination, even when simply using a color atlas, there are a few points that need to be stressed.

1. A color atlas should be selected that is universally available and that has individual copies with a high degree of agreement among them. For this, the *Munsell Book of Color* or the Maerz and Paul *Dictionary of Color* are recommended although each has its advantages for particular purposes.

2. A proper light source must be used which must be specified in any written report and must be as uniform during determinations as possible. For this, the light from a north, cloudless sky is satisfactory.

3. Masks of neutral hue and of medium value gray or black with equally sized and shaped windows for both sample and standard must be used. The colors of the masks used should be reported. The openings should be as large as feasible with the standards and samples at hand and of course must not allow any other light through but that being matched.

4. Sample and standard should be placed so that light strikes each and reflects from each in like manner.

5. Sample and standard should be placed as close together as possible.

The colors of a number of population samples of wren-tits were analyzed by these methods to select a reference series of birds showing a relatively uniform color gradient. This series was then used as a set of color standards with which to determine the position in the color gradient of other specimens of wren-tits from various localities. The assigning of code numbers of the birds in the nine steps of the gradient permitted arithmetic manipulation of these indices and hence statistical comparison of the population samples. This system served satisfactorily in description and analysis of the clinal pattern of coloration in the wren-tits of the area studied.

LITERATURE CITED

BOUMA, P. J. 1947. Physical aspects of colour. Philips Industries, The Netherlands, 312 pp.

COMMITTEE ON COLORIMETRY OF THE OPTICAL SOCIETY OF AMERICA. 1953. The science of color. Thomas Y. Crowell Co., N. Y., 385 pp.

EDITORS OF LIFE. 1944. Color. *Life,* July 3, 1944.

HAMLY, D. H. 1949. The Ridgway color standards with a Munsell notation key. *Jour. Optical Soc. Am., 39*:592–599.

HARDY, A. C. 1936. Handbook of colorimetry. Technology Press, Mass. Inst. Tech., Cambridge, Mass., 87 pp.

ILLMAN, W. I. and HAMLY, D. H. 1948. A report on the Ridgway color standards. *Science, 107*:626–628.

JUDD, D. B. 1933. The 1931 I. C. I. standard observer and coordinate system for colorimetry. *Jour. Optical Soc. Am., 23*:359–374.

JUDD, D. B. and KELLY, K. L. 1939. Method of designating colors. (*U.S.*) *Natl. Bur. Stand. Jour. Res.* (RP 1239), *23*:355–385.

MAERZ, A. and PAUL, M. R. 1951. A dictionary of color, 2nd ed. McGraw-Hill, New York, 208 pp.

MUNSELL, A. H. (1905). 1954. A color notation, Ed. 10. Munsell Color Co., Inc., Baltimore, Md., 67 pp.

——— 1929, 1942. Munsell book of color, pocket edition. Munsell Color Co., Inc., Baltimore, Md., 42 colored plates.

NEWHALL, S. M., NICKERSON, D., and JUDD, D. B. 1943. Final report of the O.S.A. subcommittee on the spacing of the Munsell colors. *Jour. Optical Soc. Am., 33*:385–418.

NICKERSON, DOROTHY. 1946. Color measurement. *U. S. Dept. Agr. Misc. Publ. 580*:1–62.

——— 1947. Interrelation of color specifications. *Paper Trade Jour.* (TAPPI Section), *125*:219–237.

RIDGWAY, R. 1912. Color standards and color nomenclature. Published by the author, Washington, D. C., 43 colored plates.

VILLALOBOS-DOMINGUEZ, C. and VILLALOBOS, J. 1947. Atlas de los colores (Portugese and English text). El Ateneo, Buenos Aires, Argentina., 74 colored plates.

DARL E. BOWERS is Assistant Professor of Biological Sciences at Mills College, Oakland, California. This paper is a contribution from the Museum of Vertebrate Zoology, University of California, Berkeley.

(*Concluded on p. 182*)

Dr. Asbjørn P. Ousdal

Patron

of the

Society of Systematic Zoology

Scottish Rite Library and
Research Department for the study of micro-fossils,
Santa Barbara, California.

Dr. Ousdal, *right*, and Mr. Ralph Hine (33°), member of the Board, Scottish Rite Temple, Santa Barbara, examining an album of Dr. Ousdal's photomicrographs.

Dr. Asbjørn P. Ousdal

The Society of Systematic Zoology welcomes as a patron Dr. Asbjørn P. Ousdal, retired physician and surgeon of Santa Barbara, California. Although Dr. Ousdal is not a systematist, he has long been interested in meteorites because of the information they may reveal about worlds other than our own, and this has led him close to taxonomy in a field of "cosmic biology" which few persons have studied.

Since his retirement in 1943, Dr. Ousdal has devoted himself assiduously to the careful study of nitrocellulose "peels" (Darrah method of 1936) of sections of stony meteorites, also known as aerolites. He has set up and endowed a well-equipped microfossil research laboratory and library in the Scottish Rite Masonic Temple at 16 East Carrillo Street in Santa Barbara.

Structures observed in certain of his preparations of sections of an aerolite found near Alamogordo, New Mexico, by Dr. H. H. Nininger, impressed Dr. Ousdal with their close resemblance to forms of vegetation inhabiting the earth today. One of these was reported on and illustrated in a paper delivered before the Botanical Society of America at its annual meeting with the Pacific Section of the American Association for the Advancement of Science in Santa Barbara in June 1953. For this, Dr. Ousdal proposed the name *Protomarsilea caelestis*.

The "megaspore" of this meteoritic "fossil" is reminiscent of those of certain living genera of pteridophytes, *Marsilea*, *Pilularis*, and *Regnellidium*. However, they are sufficiently different to preclude identification with any of these genera.

Another specimen resembles a recent fresh-water alga, *Calothrix parietina*. Dr. Ousdal's identification of this "peel" with that particular alga is in a measure descriptive of his specimen. Several competent botanists who have examined his photo-micrographs acknowledge the resemblance. Along with others, however, they find it difficult to believe that the structures can be of organic origin or that they could have existed as plants on other worlds or could have survived in recognizable form the incredible journey through space.

Dr. Ousdal defended his convictions in a later paper entitled "Apparent Function as Observed in Fossil Membranes," which was read in 1954 before another meeting of the Botanical Society on the occasion of its meeting with the American Institute of Biological Sciences at the University of Florida in Gainesville, and again in a more extended presentation, "Forever and Another Day," privately circulated.

Previously Dr. Ousdal had excavated remains of prehistoric life from partially submerged Miocene formations in the vicinity of Santa Barbara. Among these remains were fossil skulls of extinct whales. Two of these were later presented to the U. S. National Museum, one personally selected from Dr. Ousdal's collection by Dr. Alexander Wetmore, formerly director of the Museum and secretary of the Smithsonian Institution, the other at the solicitation of Dr. Remington Kellogg, present director of the Museum. They were identified by Dr. Kellogg as representatives of the Whale-bone whales, Family Cetotheriidae. As Dr. Ousdal expressed it to Dr. Wetmore, "With a little persistent effort we can unravel some of the mysteries of the past."

Some of Dr. Ousdal's researches were carried on in the geological laboratories of the University of California at Los Angeles. He also pursued graduate study in the Department of Geology at the University of Southern California, where he is a member of the local chapter of Sigma Xi.

The Society of Systematic Zoology appreciates the interest and aid of such men as Dr. Ousdal in the study of all aspects of life, now or in the past, here or elsewhere.

Structure observed in section of stony meteorite from Alamogordo, New Mexico, which simulates the recent freshwater alga, *Calothrix parietina*.

Another structure in sectional meteorite resembling spores of recent pteridophytes.

Sections by Ousdal; both greatly enlarged.

SYSTEMATIC ZOOLOGY *is honored to publish the following discussion of the nature and systematic position of the Pogonophora, the group of deuterostomes for which the author, on the basis of painstaking investigations, has recently erected the phylum Brachiata.* **A. V. IVANOV,** *Professor at the Laboratory of Invertebrate Zoology, University of Leningrad, and at the Zoological Institute, Leningrad Academy of Sciences, has prepared this article especially for the readers of this journal.*

On the Systematic Position of Pogonophora

A. V. IVANOV

IN 1954 SYSTEMATIC ZOOLOGY (*3*, pp. 69–79) published a translation by A. Petrunkevitch of my paper in Russian "New Pogonophora from Far Eastern Seas," which first appeared in the *Zoologicheskii Zhurnal* (1952, *31*, pp. 372–391). In the next issue of SYSTEMATIC ZOOLOGY (*3*, pp. 183–185) Olga Hartman, a well-known specialist in the systematics of Polychaeta, published a paper on the systematic position of Pogonophora. Hartman's most important statement runs as follows: Pogonophora represents a heterogeneous artificial group of aberrant Polychaeta, which "may in time find their affinities with several families of the sedentary polychaetous annelids."

At present I have many data, concerning 18 species of Pogonophora, belonging to 8 genera, 5 families and 2 orders. I have studied the anatomy of the following seven genera: *Siboglinum* (Siboglinidae), *Oligobrachia* and *Birsteinia* (Oligobrachiidae), *Heptabrachia* and *Polybrachia* (Polybrachiidae), *Lamellisabella* (Lamellisabellidae), *Spirobrachia* (Spirobrachiidae) on a series of sections of well-preserved specimens. Thus I have had the opportunity of throwing some light upon the principal features and the general plan of structure of the whole group, and of presenting a well-founded statement concerning the place of the group in the system of the Animal Kingdom. The communications preliminary to a comprehensive paper, which I am preparing for the press, have been already published in *Doklady Akademii Nauk USSR* (*100*, pp. 175–177, 381–383, 595–596) and will be referred to as Ivanov 1955*a*, *b*, *c*.[1]

In the present paper I am not going to give a description of the anatomy of Pogonophora, but shall restrict myself to some observations concerning the paper of my esteemed opponent.

First of all, I wish to stress that contrary to the opinion of O. Hartman, the Pogonophora constitute rather a homogeneous, completely natural group of animals. All the Pogonophora are notable for a remarkable uniformity in their general structure (see Figure 1 in Ivanov, 1955*d*). It is true that some familes have a pericardial sac adjoining the heart, and their coelomoducts of the first segment are widely set apart, while other families have no pericard, and their coelomoducts, lying in the ventral invagination of the dorsal blood vessel, are brought together. However, these distinctions by no means vitiate the architectonic uniformity of the class and are sufficient only for dividing it into two orders: Athecanephria and

[1] These three papers which appeared in DAN (*100*) in Russian have been translated by A. Petrunkevitch and published together in SYSTEMATIC ZOOLOGY (*4*:170–178). This translation is indicated in the bibliography as Ivanov, 1955*d*. *Ed.*

Thecanephria (A. Ivanov, 1955*c*, p. 596). The external morphology is also remarkably uniform. The only exception being the structure of the tentacular crown, that is the number and relative position of the tentacles and the presence or absence of connections between them. Nevertheless, the structure of every individual tentacle is principally the same in all Pogonophora, be it the sole tentacle of *Siboglinum* or one of the 223 tentacles of the complicated crown of *Spirobrachia grandis* A. Ivanov. Therefore I see no reason to consider the Pogonophora a heterogeneous artificial group, different genera of which might be derived from different ancestors.

Metamerism

The anatomical studies of a number of Pogonophora, carried out by K. Johansson (1937, 1939), M. Caullery (1944) and myself (1952, 1955*a*, *b*) indicate that these animals are undoubtedly oligomerous. Their body consists of three segments. No wonder, therefore, that all the authors, who discussed the systematic position and the structure of Pogonophora, acknowledged their oligomerous nature (E. Reisinger, 1938, p. 49; P. Uschakow, 1940, p. 76; F. Hempelmann, 1943, p. 78; V. Beklemishev, 1944, pp. 257–259, 1951, p. 5, 1952, pp. 17, 295–298; C. Davydoff, 1948, pp. 161–163; A. Pearse, 1949, p. 10; W. Ulrich, 1950, pp. 14–17; V. Dogiel, 1954, p. 250; G. de Beer, 1955, p. 888; G. Jägersten, 1956, pp. 211–252). Olga Hartman alone is an exception (1951, pp. 379–380; 1954, pp. 183–185) in that she regards the metameric arrangement of the adhesive papillae, bearing chitinized platelets, to be the manifestation of true polymetamerism (segmentation). Hartman quotes Hadži (1953, p. 153), who points out that in tubicolous Polychaeta there is a strong tendency toward the reduction of dissepiments, which is an adaptation for the sedentary mode of life.[3] Hartman considers this process to be characteristic of the evolution of Pogonophora and regards them as animals that have undergone a transition from polymerous to oligomerous condition, this transition being due to the tubicolous mode of life. In Hartman's opinion the adhesive papillae in Pogonophora are the modified parapodia, while their platelets correspond to the parapodial setae.

However, the metamerism of the adhesive papillae is remarkable for its great irregularity and inconsistency, and is pronounced only in some parts of the trunk. On the greater part of the trunk they are scattered irregularly, but are usually more numerous on the ventral side. There are considerable irregularities and individual divergencies in the paired metameric arrangement of the papillae on the anterior region of the preannular section of the trunk. For instance, a specimen of *Lamellisabella zachsi* Uschakow has the third right adhesive papilla situated opposite the second left papilla; the tenth right papilla is situated opposite the seventh left one; the twenty-first right papilla is located opposite the eighteenth left one. In another specimen the fifth right papilla is situated opposite the sixth left one, the eighth right papilla opposite the eleventh left one, the fourteenth right papilla opposite the eighteenth left one, and so on. The same may be observed in all other known species of Pogonophora (A. Ivanov, 1949, p. 81; 1952, pp. 378, 386). This metameric irregularity may be seen also in the postannular section, where the papillae usually form transverse ventral rows.

The metamerism of the polymerous Polychaeta, on the contrary, is remarkable for its regularity and consistency. It could not be otherwise, as this metamerism is a natural and inevitable consequence of the way in which the segments develop during ontogenesis. As is known, the postlarval segments, which constitute the main part of the body in Polychaeta, are always formed as a result of subterminal growth (P. Ivanoff, 1928, pp. 150–151;

[3] As I intend to show further on, this statement about the tubicolous Polychaeta is highly questionable.

1937, p. 199; V. Beklemishev, 1952, pp. 171–173). On the anterior end of the anal lobe of the metatrochophora there emerges a ring-shaped growth zone. That zone buds off segments, one after another regularly; each of these segments has its own set of organs. Therefore metamerism in Polychaeta is highly organized and perfect. Comparing metamerism in Polychaeta with that of Pogonophora, it is easy to see that they are of quite different types.

V. Beklemishev in his remarkable book *The Principles of the Comparative Anatomy of Invertebrates* (1952, pp. 153–192) presents a full study and a broad analysis of metamerism [4] in the Animal Kingdom. He indicates that there are the following three ways in which metamerism may originate (1952, p. 155):

1. The metameric readjustment of previously disarranged identical parts or organs.

As an example of such metamerism may be taken the secondary readjustment of initially scattered numerous organs in some Turbellaria (e.g. in *Procerodes lobata* O. Schmidt), as well as in many Nemertini (gonads, lateral outgrowths of intestine, and sometimes nerve commissures) and in Enteropneusta (gill-slits, intestine pores, gill blood vessels, liver outgrowths of the intestine, and gonads). This metamerism is often not yet firmly stabilized and often is still imperfect, showing some deviations from an exact metameric arrangement. Certain discrepancies in the metamerism of different systems of organs are not unusual.

It is obvious from the above that the Pogonophora display this very metamerism of readjustment in the arrangement of their adhesive papillae.

2. The metameric differentiation of body-parts or organs along the originally undifferentiated body.

Thus, the originally undifferentiated deutomerite in *Taeniocystis mira* Léger (Sporozoa, Gregarinida) is secondarily divided into a series of metameric sections. The same may be said of the metamerism in the parasitic mastigophore *Cyclonympha* (=*Teratonympha*) *strobila* Dogiel (order Hypermastigida) and also about the entirely exterior metamerism in *Moniliformis moniliformis* (Bremser) (Acanthocephala). The metameric arrangement of the cuticular formations in some Nematoda (e.g. in *Desmoscolex minutus* Claparède) is of the same pattern.

3. The joining of the formerly independent similar parts into one metamerous unit. As it was pointed out by Beklemishev (1952, p. 155) this manner of origin of metamerism is essentially different from the first two in its initial stage. In this case metamerism is developed by the joining together of independent nonmetamerous units of inferior order, but it does not manifest itself in the whole organism, formerly devoid of metamerism.

In the case of Polychaeta such nonmetameric units are the postlarval segments, every one of which develops independently from the growth zone of the metatrochophora. Among the metameric Protozoa the examples will be the parasitic Infusoria-Astomata (order Holotricha), the mastigophore *Polykrikos* (order Dinoflagellata), etc. Among the metameric Metazoa we may point out the strobilae of Scyphozoa, colonies of some Siphonophora (Physophorida of the order of Siphonanthae), temporary chains of individuals in Turbellaria, which reproduce by paratomy, such as *Catenula* and *Stenostomum* (order Notandropora), *Microstomum* and *Alaurina* (order Macrostomida), the strobilae of Cestodes, and finally the polymerous Annelida and their descendants, the Arthropoda.

Thus, the imperfect metamerism inherent to Pogonophora has nothing in common in its origin with the highly developed metamerism (segmentation) in Polychaeta.

[4] Like V. Beklemishev, I regard every regular repetition of identical organs along the body axis as representing a true metamerism.

Adhesive Papillae

Also there is no serious reason for considering the adhesive papillae of the Pogonophora as being homologous to parapodia of Polychaeta. Their only common feature is that both of them represent muscular outgrowths of the body-wall; they both have chitinoid formations. However, the papillae lack the most characteristic features of the parapodia. Their chitinized platelets represent merely some local thickenings of the epithelial cuticule. In fact, they have absolutely no resemblance to the setose sacs of the parapodia. In the anterior region of the trunk, where the papillae are somewhat larger and are metamerically arranged, the cuticular platelets are underlain by several epithelial cells, while setae of annelids, unless they are not composite, always are produced by one cell. The internal chitinoid formations, which may be compared to the supporting setae (acicula) of the parapodia, are absent.

In Pogonophora however the adhesive papillae undoubtedly serve for fixing to the internal surface of the tube, and for the support of the long body, which moves therein. Considering the similar mode of life of the Pogonophora and the tubicolous Polychaeta, it is no wonder that both possess similar, and in part similarly placed, organs of fixation and movement.

The external resemblance of the denticulate platelets on the belts (annuli) of Pogonophora to the uncini of sedentary Polychaeta [a fact which was noticed by Caullery (1944, p. 18) in *Siboglinum*], may also be easily explained by their similar mode of life. The belts in Pogonophora serve the purpose of firmly fixing the animal to the wall of the tube; it is natural that their platelets are provided with denticles. Cuticular hooks, as is well known, develop in various animals, whenever a firm attachment to the substrate is essential. It would be strange, if a tubicolous animal, possessing a powerful longitudinal musculature that instantly retracts the anterior end of its body into its tube whenever danger threatens, was not provided with means for firmly anchoring the posterior end of the body deep in the tube.

Thus, the adhesive papillae of Pogonophora by their origin are different from the parapodia of Annelida. They are new special structures characteristic of Pogonophora.

From this viewpoint it is easy to understand the characteristic features of the localization of adhesive papillae.

V. Dogiel (1936, p. 109) discovered and studied some important general principles in the development of organs. Later, in 1954, he gave a detailed analysis of those principles in his outstanding publication "The oligomerization of homologous organs, as one of the main ways in the evolution of the Animal Kingdom." Having examined and studied a vast segment of the data accumulated by modern zoology, Dogiel proved that the organs appearing *de novo* in phylogenesis, are in the majority of cases laid down in an indeterminate number (the principle of the development of organs from multiple primordia), and are at first without orderly arrangement. In their further evolution the organs become localized and their number stabilizes. Later they undergo differentiation, and diminish in number, i.e. they undergo a typical process, named by Dogiel oligomerization of homologous and homodynamic organs.

Origin from multiple primordia is highly characteristic of external organs, as well as of organs, the functions of which are connected with the environment. Dogiel (1954, pp. 1–368) analysed more than 50 cases of the phylogenetic development of organs from multiple primordia.

Turning to the question of the nature of the adhesive papillae in Pogonophora, it can easily be noticed that they possess all the characteristic features of organs originating from multiple primordia. Their total number is very large and varies not only in different species, but is also highly variable in different individ-

uals of one and the same species, i.e. the number of organs is remarkable for its instability. The overwhelming majority of papillae (on the greater part of the preannular region of the trunk) are scattered irregularly. The structure of the papillae is very simple, the papillae of different parts of the trunk being almost identical. On the anterior part of the preannular region as well as on the postannular, they have entered into the next stage of evolution and have already acquired a more or less regular metameric arrangement, although the peculiarities of their localization in these regions are different. The secondary metamerization of the papillae is evidently brought about by some functional advantages of metameric arrangement, connected with the necessity of quick movement in a narrow tube. Probably, all the papillae were scattered irregularly in the first stages of their evolution.

A comparative study of Pogonophora reveals the fact that in the primitive genera *Oligobrachia* and *Heptabrachia* [5] the anterior metamerous part of the trunk is somewhat shorter and bears a smaller number of paired papillae (from 14 to 20 pairs) than in highly specialized genera—*Lamellisabella* and especially *Spirobrachia* [in *S. grandis* A. Ivanov the number of paired papillae amounts to 220 pairs (A. Ivanov, 1952, pp. 376, 386)]. These data also confirm the opinion, that the metamerism of the papillae is a result of a secondary readjustment of the arrangement of these organs.

Reduction of Dissepiments

Now let us see whether O. Hartman's supposition concerning the reduction of the dissepiments in the body of Pogonophora (1952, p. 184) is well-founded. She tries to support her opinion by an unconvincing reference to the fact that tubicolous Polychaeta acquire, as a result of a sessile mode of life, a tendency to reduce coelomic sacs through the disappearance of dissepiments.

Let us turn to facts. In such tubicolous Polychaeta as Sabellidae and Serpulidae (order Serpulimorpha), as well as in Chaetopteridae and Hermellidae (order Spionimorpha), the dissepiments are normally developed along the entire body; there is one pair of large excretory nephridia in the thorax (with the exception of Chaetopteridae); and numerous homonomous coelomoducts and gonads are developed in the abdomen. The Terebellidae, Ampharetidae and Amphictenidae (order Terebellomorpha), all living in tubes present exceptions to this rule; their dissepiments of the thorax are reduced, except the one between the third and the fourth, or between the fifth and the sixth segments. The number of mixonephridia in the thorax varies from three to six pairs. However, even in these Polychaeta there is a complete set of dissepiments and small mixonephridia having a sexual function (E. Meyer, 1886).

In fact the disappearance of dissepiments in Polychaeta is caused not by a tubicolous but by a digging mode of life. This process is very characteristic of many digging and soil-eating Drilomorpha. The number of dissepiments in them is greatly diminished, which is an important adaptation, allowing for the pumping of the coelomic fluid from one end of the body to the other in the process of digging the soil and moving in it (L. Zenkevitch, 1944, pp. 158–159). Correlatively with the loss of dissepiments, the nephridia are reduced. This adaptation is especially well developed in Sternaspidae, which have lost dissepiments completely and retain only two pairs of mixonephridia. It is remarkable that errant Polychaeta develop the same characters convergently through a digging mode of life: so the Amphinomidae (order Nereimorpha) living within the bottom layers have not a single dissepiment. Finally,

[5] The primitiveness of some genera is shown in the comparative study of their general organization, the study of the tentacular apparatus being of vital importance (A. Ivanov, 1952, p. 389).

the Echiurida—a class highly specialized to a digging mode of life (N. Livanov, 1940, p. 146)—though descendants of polymerous Polychaeta, are also characterized by a complete loss of dissepiments.

As Pogonophora, being tubicolous animals, are not diggers, O. Hartman's speculations on the secondary reduction of their dissepiments are groundless.

The presence of only one pair of gonads and one pair of coelomoducts in the trunk (metasoma) in Pogonophora is evidence against the polymeric nature of this region of the body. The coelomoducts are very long canals, extending along almost the whole preannular section in males and along the main part of it in females. In tubicolous Polychaeta, gonads and coelomoducts or sexual mixonephridia, situated in the abdomen, are numerous and strictly metameric, as I have already mentioned.

Identity of Body Segments

It is also evident from the above that the identification of the three body segments in Pogonophora with the body regions (tegms) in sedentary Polychaeta [namely, with the head or tentacular region, thorax, and abdomen (O. Hartman, 1954, p. 184] is entirely misleading and cannot be accepted.

The comparison of the metamerism in Pogonophora as well as Enteropneusta and lower Chordata is far more interesting and well-founded. It is remarkable that Pogonophora as well as Enteropneusta undergo a secondary metamerization of the trunk (metasoma) through the readjustment of multiple organs. In fact, exactly the same phenomenon may be observed in Acrania as well. As we know, in the embryonic development of *Amphioxus* there is a stage when the ancestral trisegmental composition is clearly discernible in the structure of the embryo (MacBride, 1914, p. 605; D. Fedotov, 1923, pp. 5, 10). The anterior (proboscidal) and the middle (collar) pairs of coelomic sacs of the embryo play no important part in the organization of the adult *Amphioxus*. On the contrary, almost the entire mesoderm of the adult animal is formed by the posterior pair of coelomic sacs, homologous to the third pair of coelomic sacs of dipleurulae and to the coelom of the trunk of Hemichordata and Pogonophora. In the course of embryonic development they become elongated and undergo an incomplete metamerization, dividing into paired somites. This causes metamerism in the musculature of the adult *Amphioxus* and leads to a correlated metamerism in the nervous system and the gonads, as well as to metameric arrangement of gill slits, gill blood-vessels and excretory organs. Thus, in Acrania and consequently in Vertebrata, metamerism is of exactly the same nature as in Hemichordata and Pogonophora. Obviously, the tendency to secondary metamerization is characteristic of the lower Deuterostomia. It is independently manifested in different organs of various groups but it is always pronounced only within the trunk segment.

Organ Systems

The absence of intestine, mouth, and anus in Pogonophora is an extraordinary, but already a reliably established fact. After having studied the anatomy of a series of species belonging to different genera and families, on microtome sections of well-fixed specimens, I have no doubts concerning this problem. The cellular cord inside the ventral blood vessel, which Johansson at first mistook for intestine (1937, p. 26), and later for its rudiment (1939, p. 269), is a peculiar cordial body. Reisinger's speculations (1938, p. 49) on the probable position of the mouth and anal opening were not confirmed. The complete absence of the intestine is functionally compensated by a complex and highly peculiar tentacular apparatus, serving, in my opinion, for the gathering, digesting, and absorption of food. For the details of this matter the reader is referred to my paper (A. Ivanov, 1955*b*).

I do not consider the absence of intestine to be a primitive feature of the body organization. The ancestors of Pogonophora apparently possessed a well-developed intestine; perhaps the larva of Pogonophora, which has not been discovered yet (although its existence is highly probable), might still retain the intestine. In any case, it is evident that the absence of notochord and gill-slits is a quite natural result of the disappearance of the intestine and cannot be considered as disproving affinity between Pogonophora and Enteropneusta, or the inclusion of the Pogonophora in the Deuterostomia.

The structure of the nervous system is, naturally, extremely important. It was in the main described by Johansson (1939, p. 264), who found no traces of ventral nerve cords in it. Recently, these facts have been confirmed (A. Ivanov, 1955*a*). Hartman, however, regards the paired lateral outgrowths of the dorsal brain as the origin of the ventral cords. This is a misunderstanding. These lateral outgrowths are the nerves to the tentacles. In *Siboglinum,* which has a single tentacle, only one such nerve issues from the brain and that on the left side of the body. This proves, incidentally, that in this genus only one left tentacle of the whole tentacular crown has been retained. All Pogonophora possess an unpaired dorsal nerve cord, which is easily discerned in the sections, almost up to the posterior end of the body (A. Ivanov, 1955*a*, p. 176).

The histological structure of the nervous system is very similar to that of Enteropneusta. It is entirely situated in the epithelium of the integument as is characteristic of lower Deuterostomia. It is true that in primitive and small Annelida, the nervous system is also located in the epithelium (*Dinophilus, Polygordius, Protodrilus,* some Spionidae and Syllidae, *Aeolosoma* of the Oligochaeta), but in sedentary tubicolous Polychaeta it is always subepithelial.

Hartman considers the presence of a single pair of thoracic (mesosomal) nephridia as a common feature typical both for Pogonophora and tubicolous Polychaeta. But it certainly has no phylogenetic significance, and does not indicate any affinity. Among the tubicolous Polychaeta, the character in question appeared independently at least twice: firstly in Hermellidae (order Spiomorpha), and secondly in Sabellidae and Serpulidae, the latter belonging to quite a different order of Serpulimorpha. The reason for this convergence is obvious; it depends on their similar modes of life. The representatives of the above-mentioned families protrude the anterior part of the body from the tube, and withdraw it only in case of danger. Naturally, of numerous thoracic nephridia they have retained and developed only that pair, the position of which provides for excretion directly into the water, thus avoiding the contamination of the tube. Contrariwise, those tubicolous Polychaeta (Chaetopteridae) that never protrude from the tube but create a constant current of water through the tube, have completely lost their thoracic nephridia (Beklemishev, 1952, p. 198).

As is well known, Phoronoidea, which live in tubes, and Bryozoa Phylactolaemata, which are enclosed in cistids, also possess a pair of nephridia, which is situated in the anterior end of the body and there opens externally. Both can extend the anterior part of the body. Finally, Sipunculida, which live in tubes, also possess similarly located nephridia.

Thus, organs of excretion that open on the anterior end of the body, have developed independently in different tubicolous animals. The nephridia of Pogonophora, lying in the anterior section of the body, are only analogous to the thoracic nephridia of Serpulimorpha and Hermellidae, and cannot serve as proof of their affinity with these Polychaeta.

Besides, there are many reasons to consider the nephridia of Pogonophora as coelomoducts of the first segment (prosoma). In this the Pogonophora resemble the Hemichordata (Enteropneusta and Pterobranchia), which possess modified

prosomal coelomoducts in the form of one or two troboscidial pores. The thoracic nephridia of Hermellidae and Serpulimorpha are mixonephridia, i.e. they are of a different nature (Goodrich, 1945, p. 295).

The development of the tentacular crown also does not provide any convincing proof in favour of phylogenetic affinities of Pogonophora and Serpulimorpha. The tentacles of Pogonophora are so peculiar, that it is unlikely that in the whole of the Animal Kingdom there are any organs resembling them. They differ markedly from the pinnate tentacle-like palps of Serpulimorpha; their thinnest pinnules are formed by a single cell penetrated by intracellular blood capillaries (A. Ivanov, 1955*b*). The functions of the tentacles in both Pogonophora and Serpulimorpha include respiration and the collection of food particles from the surrounding water; but in addition the tentacles of Pogonophora digest and absorb this food. However, the structure as well as the functions of the tentacles of Pogonophora might have originated secondarily, as a consequence of the reduction of intestine.

The presence of the tentacular crown on the anterior end of the body in a sedentary animal is in itself so common that it cannot be considered a character of phylogenetic significance. Actually, the polyps of Hydrozoa and Anthozoa, some sedentary Rotatoria (*Stephanoceros*), Kamptozoa, Phoronoidea, Bryozoa, many Polychaeta Sedentaria, Pterobranchia and even some Ascidia (*Octacnemida, Hexacrobylus*, etc.) are also provided with a crown of tentacles. The lower sessile Echinodermata (Pelmatozoa) are also provided with tentacle-like appendages—brachioles (Cystoidea and Blastoidea), or hands (Crinoidea). Because of the development of the tentacular crown during the sedentary mode of life, animals systematically remote have come to have a polyp-like or serpula-like appearance. Pogonophora prove to be no exception to this rule.

Summary and Conclusions

Finally, I shall enumerate the peculiar characters of the organization of the Pogonophora, which prove with little doubt their affinities with the Deuterostomia, and contradict strongly their affinities with Annelida:

1. The trisegmental composition of the body.
2. The presence of an unpaired dorsal nerve cord.
3. The absence of ventral nerve cords.
4. The presence of the heart.
5. The presence of the pericardial sac.
6. The presence of a pair of coelomoducts in the first segment.
7. The presence of a pair of gonads in the third segment.
8. The development of a rudimentary metameric arrangement within the elongated third segment.

What is said above is sufficient to prove that Pogonophora have nothing in common with Annelida (tubicolous Polychaeta). The resemblance between these groups, which seems to be very great at first glance, is entirely superficial and represents convergences attributable to a similar mode of life in a tube. The entire organization of the Pogonophora proves their affinity with Deuterostomia, among which they should be regarded as a separate phylum (A. Ivanov, 1955*c*).

REFERENCES

BEKLEMISHEV, V. N. 1944. The principles of the comparative anatomy of invertebrates. (First ed.) Moscow. Pp. 1–492. (In Russian.)

——— 1951. On the construction of a phylogenetic system for animals; Deuterostomia, their origin and composition. *Uspekhi sovr. biologii, 32*:256–270. (In Russian.)

——— 1952. The principles of the comparative anatomy of invertebrates. (Second ed.) Moscow. Pp. 1–698. (In Russian.)

CAULLERY, M. 1914. Sur les Siboglinidae, type nouveau d'invertébrés recueilli par l'expédition du Siboga. *C. R. Acad. Sci. Paris, 153*:2014–2017. Also, *Bull. Soc. Zool. France, 39*:350–353.

——— 1944. *Siboglinum* Caullery. Type nouveau d'invertébrés d'affinités a préciser.

Siboga Exped. Leiden, 138, Monogr. 25 bis, pp. 1–26.

DAVYDOFF, C. 1948. Contribution à la connaissance de Siboglinum Caullery. *Bull. biol. France, Belgique, 82*:141–163.

DE BEER, G. 1955. The Pogonophora. *Nature, 176*(4488):888.

DOGIEL, V. A. 1936. The oligomerization of homologous organs as one of the processes of evolution in the Animal Kingdom. *Arkhiv anat. gistol. i embryol., 15*:101–114. (In Russian.)

——— 1954. The oligomerization of homologous organs as one of the main ways in the evolution of animals. Leningrad. Pp. 1–368. (In Russian.)

FEDOTOV, D. M. 1923. Concerning the homologies of the coeloms of Echinodermata, Enteropneusta and Chordata. *Izvestia biologicheskogo nauchno-issledovatelskogo instituta i biologicheskoi stanzii Permskogo gosudarstvennogo universiteta, 2*:1–11. (In Russian.)

GOODRICH, E. S. 1945. The study of nephridia and genital ducts since 1895. *Quart. Journ. Microsc. Sci., 86*(Parts II, III, IV):113–392.

HADŽI, J. 1953. A reconstruction of animal classification. *Syst. Zool., 2*:145–154.

HARTMAN, O. 1951. Fabricinae in the Pacific. *Pacific Science, 5*:379–380.

——— 1954. Pogonophora Johansson 1938. *Syst. Zool., 3*:183–185.

HEMPELMAN, F. 1943. Pogonophora. Morphologie und Entwicklungsgeschichte der Wirbellosen. *Fortschr. Zool., 7*:78–79.

IVANOFF, P. P. 1928. Die Entwicklung der Larvalsegmente bei den Anneliden. *Zeitschr. Morph. Ökol., 10*:62–161.

——— 1937. General and comparative embryology. Moscow and Leningrad. Pp. 1–809. (In Russian.)

IVANOV, A. V. 1952. New Pogonophora from Far Eastern Seas. *Zoologicheskii Zhurnal, 31*:372–391. (In Russian.)

——— 1954. New Pogonophora from Far Eastern Seas. *Syst. Zool., 3*:69–79. Translation by A. PETRUNKEVITCH of Ivanov, 1952.

——— 1955*a*. The main features of the organization of Pogonophora *Doklady Akademii Nauk USSR, 100*:175–177. (In Russian.)

——— 1955*b*. On external digestion in Pogonophora. *Doklady Akademii Nauk USSR, 100*:381–383. (In Russian.)

——— 1955*c*. On the assignment of the Class Pogonophora to a separate Phylum of Deuterostomia—Brachiata A. Ivanov, phylum nov. *Doklady Akademii Nauk USSR, 100*: 595–596. (In Russian.)

——— 1955*d*. Pogonophora. Translation by A. PETRUNKEVITCH of Ivanov 1955*a,b,c*. *Syst. Zool., 4*:170–178.

JÄGERSTEN, G. 1956. Investigations on *Siboglinum ekmani,* n. sp. encountered in the Skagerak. *Zool. Bidrag från Uppsala, 31*:211–252.

JOHANSSON, K. 1937. Über *Lamellisabella zachsi* und ihre systematische Stellung. *Zool. Anz., 117*:23–26.

——— 1939. *Lamellisabella zachsi* Uschakow, ein Vertreter einer neuen Tierklasse Pogonophora. *Zool. Bidrag från Uppsala, 18*: 253–268.

LIVANOV, N. A. 1940. Class Echiuroidea. Manual of zoology, vol. 2. Moscow-Leningrad. Pp. 137–156. (In Russian.)

MACBRIDE, E. 1914. Text-book of embryology, vol. I. Invertebrata. Pp. 1–692. Macmillan Co., London.

MEYER, E. 1886–87, 1888. Studien über den Körperbau der Anneliden I–III, IV. *Mitteilungen Zool. Stat. Neapel, 7, 8*:593–741, 462–662.

PEARSE, A. 1949. Zoological names. A list of phyla, classes, and orders. For the American Association for the Advancement of Science. Durham, N. Carolina, p. 10.

REISINGER, E. 1938. Pogonophora. Morphologie und Entwicklungsgeschichte der Wirbellosen. *Fortschr. Zool., 3*:49–50.

ULRICH, W. 1950. Ueber die systematische Stellung einer neuen Tierklasse (Pogonophora K. E. Johansson). *Sitzungsber. Deutschen Akad. Wiss. Berlin Math.-natur. Kl.,* 1949 (2):1–25.

USCHAKOW, P. W. 1940. A new group of oligomerous worms (Pogonophora) from the abyssal depths of the Okhotsk Sea and the Polar Basin. *Priroda, 3*:76–77. (In Russian.)

ZENKEVITCH, L. A. 1944. Outline of the evolution of locomotor apparatuses of animals. 1. The general principles of the evolution of locomotion in animals. *Zhurnal obshehei biologii, 5*: 129–171. (In Russian.)

Relationships of the Thrush Genera *Catharus* and *Hylocichla*

WILLIAM C. DILGER

DURING the course of investigations designed to gain knowledge concerning the reproductive and ecological isolating mechanisms operating in the genus *Hylocichla*, information came to light which makes a contribution to a better understanding regarding its relationships (Dilger, 1956*a*, 1956*b*).

There has been frequent and justified criticism of many systematic ornithological papers at the generic and higher levels because of their heavy reliance on one criterion. Knowledge about birds, at least most North American and European species, has reached the point where "one criterion systematics" is no longer necessary. The following is an example of how behavioral, anatomical, ecological and serological information may be brought to bear on the uncertain relationships of a group.

There are two principal problems regarding the systematics of *Hylocichla*. One involves the generic relationships and the other the tribal relationships. The relationships on both levels have been the subjects of much difference of opinion. On the generic level some prefer to maintain the genus *Hylocichla* (e.g., A.O.U., 1931) and others prefer to consider it congeneric with *Catharus* (e.g., Ripley, 1952). Most European workers think of *Hylocichla* as being allied to the true thrushes of the genus *Turdus* and some (e.g., Dorst, 1950) even think that *Hylocichla* should be considered congeneric with *Turdus*. Others (e.g., Mayr, personal communication) think of *Hylocichla* as perhaps be-

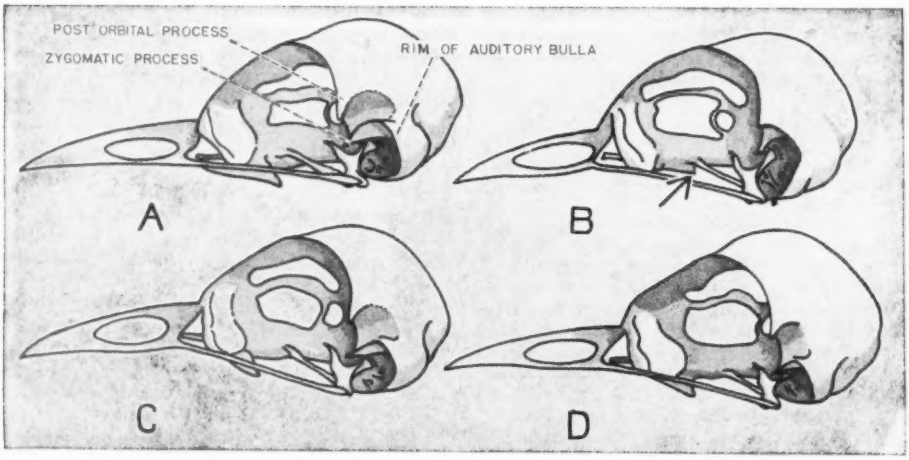

FIG. 1. Semidiagramatic views of the skulls of: *A, Turdus migratorius; B, Erithacus rubecula; C, Hylocichla mustelina;* and *D, Catharus minimus.* Note the confluence of the rim of the auditory bulla with the postorbital process, and the abrupt junction of the palatine with the basisphenoidal rostrum (arrow) in *Erithacus.* The rims of the bullae are confluent with the zygomatic processes, and the palatines gradually join the rostra in the others. For ease of comparison these skulls have been drawn as if they were all about the same size.

ing more closely allied to the chat-like thrushes such as *Erithacus* and *Luscinia*.

Tribal Relationships

I agree with Beecher (1953) who has divided the thrushes into two subfamilies; the chats, Saxicolinae and the thrushes, Turdinae. He also includes with his Turdidae two other groups that are traditionally regarded as families (his Miminae and Cinclinae). These need not concern us here. Ripley (1952) also divides the thrushes into two groups which he terms tribes, as he regards the thrushes as a subfamily, Turdinae, of the Muscicapidae, the primitive insect eaters. Mayr and Amadon (1951) also support this position, although they include several more tribes. Since Ripley does not actually name his two tribes, I will refer to them as the Turdini (true thrushes) and the Saxicolini (chat thrushes). These are the equivalent of Beecher's (1953) Turdinae and Saxicolinae.

It is notoriously difficult to unearth dependable characters upon which to base passerine relationships. Beecher bases his distinction between the chat thrushes and true thrushes mainly on the character of the jaw muscles. The true thrushes have a proportionately heavier jaw musculature plus a pinnately fibered component missing in the chats with their relatively weaker jaw muscles. My dissections have verified this. I examined examples of fifty-six forms preserved in alcohol and seventy-one forms represented as skeletons. These represented both saxicoline and turdine species.

During the course of my investigations three other characters were found which seem to be of value and which support Ripley's (1952) and Beecher's (1953) grouping. Two of these characters are skeletal, and the other involves a feature of the pectoral musculature. The skeletal characters involve the auditory bullae and the palatines. Turdine thrushes have the rims of the auditory bullae confluent with the zygomatic processes of the orbits, while saxicoline thrushes, for the most part, have these rims confluent with the postorbital processes of the orbits (Fig. 1 and Table I). Some chats have a modification of this condition where the rim approaches the postorbital process but does not quite reach it.

Turdine thrushes have the palatines gradually sloping to grasp the basisphenoidal rostrum, while chats have the palatines abruptly joining the rostrum (Fig. 1). *Myadestes genibarbis* and *M. townsendi* (the only two representatives of the genus available to me) have the palatine characters of turdine thrushes, as do *Sialia sialis* and *S. currucoides* (again, the only two representatives of the genus available to me). These four forms also have the auditory bulla character of turdine thrushes. However, these species resem-

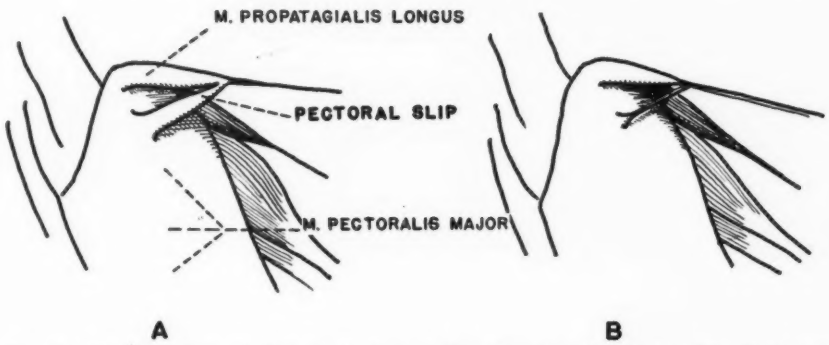

FIG. 2. Ventral view of the pectoral area in: *Turdus migratorius* (Turdini), *A*, and *Luscinia megarhynchos* (Saxicolini), *B*. Note the muscular condition of the pectoral slip in *T. migratorius* and the tendinous condition of this slip in *L. megarhynchos*.

ble chats in the character considered next.

All of the preserved thrushes which I examined had a slip from the *M. pectoralis major* to the *M. propatagialis longus* (Fig. 2). Turdine thrushes have this slip heavily muscled with the tendinous connection at a minimum. Chat thrushes have this slip largely tendinous (Table I).

All of the species of *Hylocichla* (*mustelina, fuscescens, guttata, ustulata* and *minima*) demonstrates these three characters in typical turdine fashion (Table I).

Discussion. Characters used at the tribal level have to be relatively conservative if they are to be of use. The skull characters mentioned above may possibly be the result of rather rapid modifications brought about by selection operating on the feeding behavior. Jaw muscles have been criticised (Tordoff, 1954) as a character upon which too heavy a reliance may be placed. There is no doubt that the jaw musculature, like the structure of the bill, is intimately associated with feeding behavior. It is commonly understood that the bill is extremely plastic from an evolutionary standpoint, and hence of limited value as a taxonomic character even at

TABLE I—CONDITIONS OF THE AUDITORY BULLAE, PALATINES AND PECTORAL SLIP IN VARIOUS SPECIES OF THRUSHES.

SPECIES	PECTORAL SLIP	AUDITORY BULLA	PALATINES
Turdus migratorius	M	Z	G
T. albicollis	—	Z	G
T. nudigenis	—	Z	G
T. rufiventris	M	Z	G
T. serranus	—	Z	G
T. nigrescens	—	Z	G
T. mupipensis	—	Z	G
T. viscivorus	M	Z	G
T. ericetorum	M	Z	G
T. musicus	M	Z	G
T. pilaris	M	Z	G
T. naumanni	—	Z	G
T. ruficollis	—	Z	G
T. obscurus	M	Z	G
T. kessleri	—	Z	G
T. rubrocanus	—	Z	G
T. poliocephalus	M	Z	G
T. merula	M	Z	G
T. torquatus	M	Z	G
T. cardis	—	Z	G
T. libonyanus	M	Z	G
T. olivaceus	M	Z	G
Hylocichla mustelina	M	Z	G
Catharus fuscescens	M	Z	G
C. guttatus	M	Z	G
C. ustulatus	M	Z	G
C. minimus	M	Z	G
C. dryas	M	Z	G
C. occidentalis	M	Z	G
C. aurantiirostris	M	Z	G
Zoothera dauma	M	Z	G
Z. citrina	M	Z	G
Z. sp.	M	Z	G
Myiophoneus caeruleus	T	Z	G
Monticola saxatilis	T	P*	G
M. brevipes	T	P*	G
Oenanthe pileata	T	P	A
O. monticola	T	P	A
O. oenanthe	T	P	A

the generic level. The two skull characters mentioned above may also be subject to this plasticity. The palatine shapes are probably responses to the type of the *pterygoideus* muscle complex and the two auditory bullae rim types are responses to the types of jaw-adductor musculature characteristic of the two tribes. The turdine type allows ample room for attachment of the large mandibular adductors, and the saxicoline type precludes the possibility of such extensive attachment surfaces for the mandibular adductors. This may be just another way of saying that the jaw musculature of turdines is relatively more massive than that of the saxicolines.

It would seem, then, that the condition of the auditory bullae are of no greater value than are the jaw muscles. There is one observation, however, that suggests that the condition of the auditory bullae may be of greater taxonomic value than are the jaw muscles. Although it is generally true that turdine forms have heavier jaw musculature than have the chats, there are some turdine thrushes that have lighter jaw musculature (e.g., *H. minima*

TABLE I—*Continued*

SPECIES	PECTORAL SLIP	AUDITORY BULLA	PALATINES
Myrmecocichla arnotti	T	P	A
M. nigra	T	P	A
Saxicola caprata	T	P	A
S. torquata	T	P	A
Cercomela familiaris	T	P	A
Stizorhina fraseri	T	P	A
Myadestes genibarbis	T	Z	G
M. townsendi	T	Z	G
Enicurus maculatus	T	P	A
E. scouleri	T	P	A
Siala currucoides	T	Z	G
S. sialis	T	Z	G
Myiomela frontalis	T	P	A
Phoenicurus auroreus	T	P	A
P. schistoceps	T	P	A
P. frontalis	T	P	A
P. phoenicurus	T	P	A
Copsychus saularis	T	Z	—
C. malabaricus	T	P*	A
Cichladusa arquata	T	P	—
Cossypha sharpei	T	P	A
C. niveicapilla	T	P*	A
C. caffra	T	P	A
Erithacus rubecula	T	P	A
E. indicus	T	P	A
Tarsiger cyanurus	T	P	A
Luscinia calliope	—	P	A
L. megarhynchos	T	P	A
L. luscinia	—	P	A
Erythropygia barbata	T	P*	A
Brachypterx montana	T	P*	A

M = Pectoral slip muscular
T = Pectoral slip tendinous (Fig. 2)

Z = Rim of auditory bulla joins zygomatic process
P = Rim of auditory bulla joins postorbital process
P* = Rim of auditory bulla falls short of postorbital process (Fig. 1)

G = Palatines join basisphenoidal rostrum gradually
A = Palatines join basisphenoidal rostrum abruptly (Fig. 1)

bicknelli) than some of the chats have (e.g., *Enicurus maculatus*). These chat-like forms that have developed a somewhat heavier musculature than have their close relatives, gain the extra surface of origin, not by developing an auditory bulla rim which swings down to join the zygomatic process, but by keeping its postorbital attachment and having the rim pushed backward to some extent. This suggests that the rim of the auditory bullae may be a more conservative character than the jaw musculature, and hence of greater value systematically.

I have tried to correlate the pectoral slip character with some characteristic behavior in order to associate it with possible selective pressures. It is not simply correlated with size, since small turdine forms such as *H. minima bicknelli* have the typical muscular condition while the large *Myiophoneus caeruleus* has an extensive tendinous condition characteristic of the usually smaller chats. Nor is it correlated with feeding habits or with types of flight. Turdine species have a characteristic "soft" flight, whereas chats typically have a rather rapid wing beat as do most other small birds. Both *Myiophoneus* and *Sialia* have tendinous slips but have the "soft" flight typical of turdine forms. It may be that this character is truly conservative and of correspondingly greater value systematically. It is interesting to note that this character is much more consistent with the previous ideas of thrush tribal relationships than are the two skull characters (Table I).

I feel that the placement of *Hylocichla* with the true thrushes is strengthened by the three additional characters discussed above. *Hylocichla* should be considered as belonging to the tribe Turdini in the subfamily Turdinae of the family Muscicapidae.

Generic Relationships

Ridgway (1907, p. 19) may have been the first to suggest the close affinity of *Hylocichla* and *Catharus*. This opinion has been shared by many since that time but they were not published as being congeneric until Ripley (1952) did so. I believe his position to be the correct one.

The principal characters which have traditionally separated *Catharus* from *Hylocichla* are the much larger tenth (rudimentary) primary of *Catharus*, and differences in limb proportions. *Catharus* species typically have relatively longer legs and shorter wings than do the *Hylocichla* species. All of these characters have been shown to be highly adaptive and are responses to feeding and flying habits (Dilger, 1956*b*). The species of *Hylocichla*, breeding throughout most of forested North America, are highly migratory. Some (e.g., *ustulata* and *minima*) migrate from northern North America to northern South America. Their wings are relatively long and pointed with a tendency toward a reduction of the tenth primary. The *Catharus* species, being relatively sedentary southern forms, are not as well adapted for sustained flight as are their northern relatives. Their wings are shorter and more rounded and have much larger tenth primaries. The *Hylocichla* species with the shortest migration route, *guttata*, has the tenth primary longer than those of its relatives. In this respect it approaches *Catharus*, and Ripley (1952) has commented on this.

There is a tendency for variation in the tenth primary among species within other genera which have both a migratory and non-migratory group of species. For example, *Turdus*, a widespread thrush genus, has northern migratory forms and southern sedentary ones. For instance, *Turdus migratorius* and *T. iliacus* are migratory and have short tenth primaries and *Turdus nudigenis* and *T. jamaicensis* are sedentary and have relatively much longer tenth primaries.

Aside from the differences in the tenth primary and in limb proportion which have been discussed, these forms exhibit a remarkable similarity. None of my investigations of skeleton or muscle showed

any significant differences between *Catharus* and *Hylocichla.*

All are rather small, ground inhabiting forms which demonstrate a strong similarity in general biology, including nest construction and development of young. I have in my possession a nest and eggs of *Hylocichla guttata,* collected near Ithaca, New York by William J. Hamilton III, and a nest with eggs of *Catharus o. occidentalis,* collected in Mexico by Walter Bock. These two nests with their eggs are so similar that they could easily be imagined the work of one bird! I have talked and corresponded with many people who have an intimate knowledge of *Catharus* in the wild. They are unanimous in the opinion that the two genera are remarkably similar. I am especially grateful for the information given to me in this connection by Dr. Alexander Skutch and by Joyce LeFebvre.

It is true that there is some divergence between these two groups in the matter of the color of the soft parts (*Catharus* species frequently have brilliant yellow or orange eyelids, bills and feet). These portions are usually rather somber in *Hylocichla,* although *H. minima bicknelli* has a brilliant yellow basal portion of the mandible, and eyelids narrowly edged with yellow. These characters are probably species specific signal characters, at least in part. Most of the important species specific signal characters of *Hylocichla* are vocal (Dilger, 1956*a*), hence the visual ones are reduced to a minimum. In *Hylocichla* the males arrive on the breeding grounds ahead of the females, which upon arrival have to find males of their own species. The habitats in which these species occur are characterized by dense vegetation, and visibility is limited. This is probably why the main species specific signal characters in this group are vocal rather than visual. *Catharus* species, being on their breeding grounds for the most part the year around, probably have less difficulty in finding mates and hence can utilize visual signals to a greater advantage. This may be the main reason that patches of brilliant color have been developed in *Catharus.* In both genera, however, vocal signals are probably the most important species specific signals. The comparatively minor differences in plumage pattern and color exhibited by *Catharus* and *Hylocichla,* both of which are essentially cryptically colored, may be disposed of in the same manner as the soft part colors discussed above.

Hylocichla mustelina

A misfit in the rather homogeneous *Catharus-Hylocichla* assemblage is the Wood Thrush, *H. mustelina.* This species bears a close resemblance to members of the genus *Turdus;* especially to *T. musicus,* the European Song Thrush. It is this resemblance that has been largely responsible for some (e.g., Dorst, 1950) proposing to combine *Hylocichla* with *Turdus.* The Wood Thrush builds a nest that is typical of those built by many *Turdus* species. Much mud is incorporated and the eggs as well as the nest closely resemble those of the American Robin, *T. migratorius.*

Investigations into the hostile behavior patterns of *mustelina* demonstrate a great difference between it and the other *Hylocichla* species, which are all essentially similar (Dilger, 1956*a*). Preliminary investigations into the hostile behavior of the American Robin by Ficken, Sauer and Dilger (1955) indicate that the patterns of hostile behavior of this species are much nearer to those of *mustelina* than *mustelina* is to the other species of *Hylocichla.* Various fluffings of the plumage are characteristic of the aggressive displays of both the American Robin and the Wood Thrush. Both have a posture—elicited by a sudden and simultaneous strong stimulation of the attack and escape drives—which I have termed the Horizontal Fluff posture (Fig. 3). The other *Hylocichla* species do not have a similar posture. These latter do have a behavior pattern termed Foot Quivering in which the feet are alternately and rapidly quivered against the substrate.

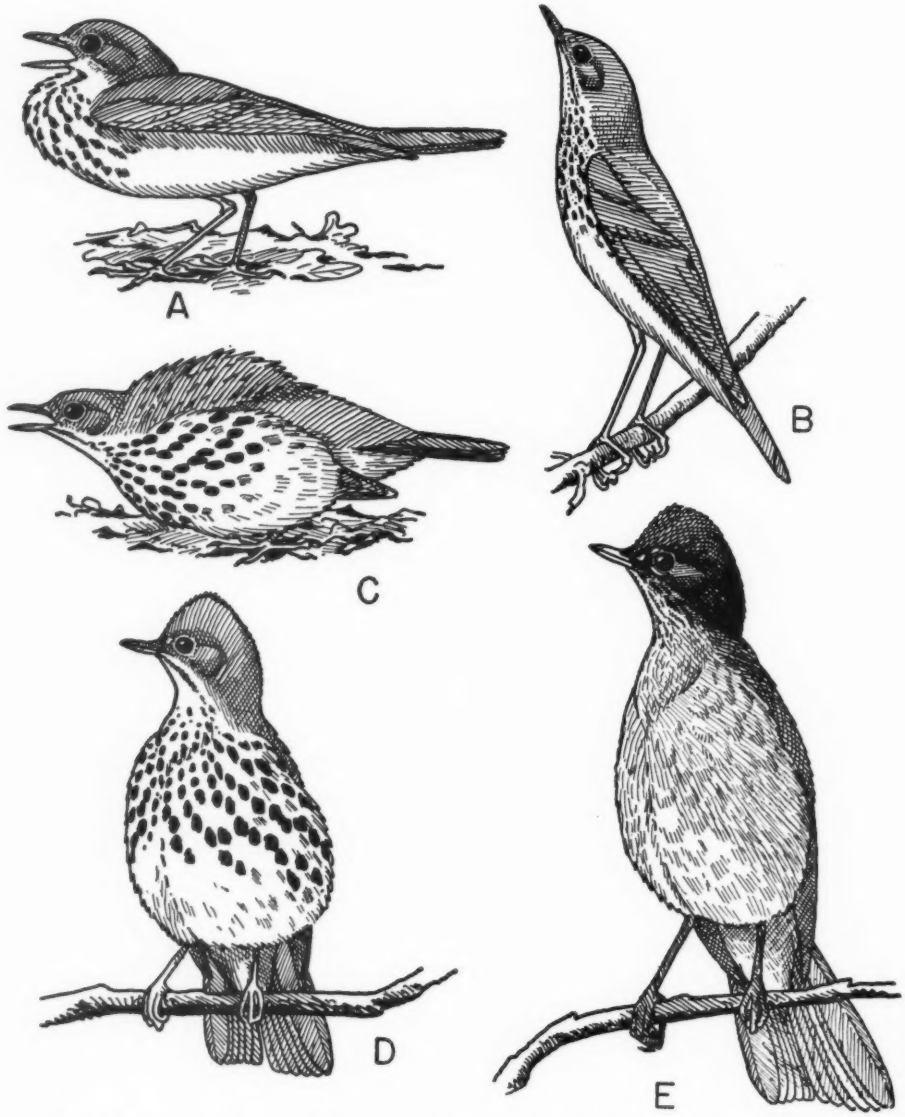

FIG. 3. Various postures indicative of hostile motivation in *Hylocichla*, *Catharus* and *Turdus*. *A*, Withdrawn posture of *Catharus fuscescens*, *C. guttatus*, *C. ustulatus* and *C. minimus*. *B*, Upward posture of these same species. The above two postures are not used by *Hylocichla mustelina* or by *Turdus migratorius*. *C*, the Horizontal Fluff posture of *H. mustelina* and *T. migratorius*. This posture is not used by the *Catharus species D*, the Spread posture of *H. mustelina* and the similar, *E*, Fluff posture of *T. migratorius*. These postures also are not used by the *Catharus* species.

This is indicative of a low, general motivation of both the attack and escape drives, and probably has originated and become ritualized from intention movements to attack (move forward) and to escape (retreat) at the same time. *Hylocichla mustelina* and *T. migratorius* do not have this display. Both *T. migratorius* and *H. mustelina* very noisely and vigorously defend their nests against predation. This is not typically true of the others.

Unfortunately, I know little about the hostile behavior of the Song Thrush, *T. musicus*. Ripley (1952) believes the resemblance between this species and *mustelina* to be "one of parallelism in external appearance only." He goes on to say that the Wood Thrush has a more slender bill and legs (which are adaptations to its feeding habits) and that the Song Thrush has *"the display"* (italics mine) on the ground while that of the Wood Thrush is in flight. Actually, the Wood Thrush has many displays, as do other birds, and most of them occur while the bird is perched (Dilger, 1956*a*). The same is no doubt true for the Song Thrush.

It is true that the foraging behavior of *H. mustelina* and *T. migratorius* is somewhat different. Robins typically run about on lawns, or other open areas, pause, peer and seize earthworms which they then pull from the ground and eat. Wood Thrushes forage on the forest floor or at the forest edge. This feeding site is characteristically covered with leaves and other detritus over which *mustelina* hops, flipping aside the leaves with its bill, and seizing the invertebrate food thus uncovered. These differences in feeding behavior are no different than one would expect of related species occupying different niches. At any rate wild Robin populations living in forested areas forage much in the fashion of the Wood Thrush; hopping from place to place and throwing aside the detritus of the forest floor with their bills. It is interesting to note here that differences in the feeding behavior among some of the rest of the genus *Hylocichla* are far greater than the difference between those of the Robin and Wood Thrush. For instance, *H. ustulata*, the Olive-backed Thrush, predominately forages in the foliage high in the trees, where it captures insects both in the foliage and on the wing. The Hermit Thrush, *guttata*, feeds on the ground, making long springing hops and flipping aside the leaves with its bill in its characteristic fashion.

Serological investigations, kindly done by Dr. Alan Boyden and Mr. T. K. R. Bourns of Rutgers University, show a strong similarity between the muscle and blood proteins of *H. mustelina* and *T. migratorius*. Again, these two species are closer to each other than *mustelina* is to the remaining four species of *Hylocichla*. These serological findings will be published in the near future by Bourns.

Summary

I believe, on the basis of this evidence, that *H. mustelina* is not particularly closely related to the other four species currently placed in *Hylocichla*, which are undoubtedly congeneric with *Catharus*. *Hylocichla mustelina* is the type species of its genus. I prefer to leave it alone in *Hylocichla*, although further investigation will probably indicate that it is best considered as *Turdus*.

Hylocichla mustelina is thus left in *Hylocichla* while the remainder of the genus (*fuscescens, guttata, ustulata* and *minima*) should be placed (as Ripley, 1952, has done) with *Catharus*, the older name, and all considered true thrushes in the tribe Turdini rather than chats, Saxicolini.

LITERATURE CITED

American Ornithologists' Union. 1931. Check-List of North American birds. 4th edition. (Amer. Ornith. Union, Lancaster, Pa.) xx + 526 pp.

Beecher, W. J. 1953. A phylogeny of the oscines. *Auk, 70*:270–333.

Dilger, W. C. 1956*a*. Hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus and Hylocichla. Auk, 73*:313–353.

——— 1956*b*. Adaptive modifications and ecological isolating mechanisms in the avian genera *Catharus* and *Hylocichla*. *Wilson Bull.*, *68*:171–199.

DORST, J. 1950. Considerations systematiques sur les grives du genre *Turdus* L. *Oiseau et R.F.O.*, *20*:212–248.

FICKEN, M., SAUER, M., and DILGER, W. C. 1955. Notes on the hostile behavior of the American Robin, *Turdus migratorius*. MS.

MAYR, E. and AMADON, D. 1951. A classification of recent birds. *Amer. Mus. Novitates*, No. 1496:42 pp.

RIDGWAY, R. 1907. The birds of North and Middle America, *Bull. U. S. Nat. Mus.* *50*(4):xxii + 973 pp.

RIPLEY, S. D. 1952. The thrushes. *Postilla*, No. 13. 48 pp.

TORDOFF, H. B. 1954. Relationships in the New World nine-primaried oscines. *Auk*, *71*:273–284.

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Methods of Color Determination

(*Concluded from p. 160*)

APPENDIX

SAMPLE CALCULATION FROM DISK COLORIMETER DATA OF SPECIMEN 9

DISK PAPER VALUES

	MUNSELL NOTATION	TRISTIMULUS VALUES WITH REFERENCE TO ILLUMINANT C X	Y	Z	PER CENT OF PAPER IN MIXTURE	$X \times$ PER CENT	$Y \times$ PER CENT	$Z \times$ PER CENT
(red)	5 YR 4/8	.1676	.1414	.0499	47	.07877	.06646	.02345
(yellow)	5 Y 6/8	.2839	.2965	.0623	10	.02839	.02965	.00623
(black)	Neutral 2/	.0294	.0302	.0341	37	.01088	.01117	.01262
(white)	Neutral 9/	.7119	.7286	.8527	6	.04271	.04372	.05116
				Totals:	100	.16075	.15100	.09346

The last three totals ($=X'$, Y', Z') represent the tristimulus values for the mixed color:

Then,

$$X' + Y' + Z' = .40521$$

and,

$$x = \frac{X'}{X' + Y' + Z'} = \frac{.16075}{.40521} = .3967$$

$$y = \frac{Y'}{X' + Y' + Z'} = \frac{.15100}{.40521} = .3726$$

The values x and y are fractional tristimulus expressions for the mixed color and can be used with an I.C.I. chromaticity diagram to give psycho-physical descriptions of the color in terms of dominant wavelength and purity with Y as above (15.10%) for brightness. By using the tables and charts published by Newhall, Nickerson, and Judd (1943) or Nickerson (1946) they can be converted into Munsell terms of hue, value, and chroma. These calculations for specimen 9 give Munsell values of 8.4 YR 4.4/3.3 as shown in Table V.

Points of View

A Case for the Trinomen

In recent months the long-established custom of nomenclatural recognition of subspecies has received severe criticism, calling either for drastic revision of the customary definition of subspecies (Edwards, *Syst. Zool., 3*:1–20, 1954), or for outright discard of the category (e.g., several papers in *Systematic Zoology*, viz: Wilson and Brown, *2*:97–110; Peters et al., *3*:97–125; Gosline, *3*:92–94; see Mayr, *3*:87 for other references). The viewpoints expressed have much merit, but in our opinion they do not render the subspecies system wholly obsolete, although little defense for it has been expressed (e. g. Mayr, *Syst. Zool. 3*:87–88, 1954; Parkes, *Syst. Zool., 4*:35–40, 1955). The practice of subspecies recognition admittedly does require revision, but the constructive criticism received in the past may readily and dangerously be misconstrued as indicating that the subspecies concept itself is spurious. We believe on the contrary that an impregnably strong case can be made for the subspecies, essentially as at present understood, and that it should be expressed for the benefit of undecided taxonomists and for non-taxonomists who find the arguments attractive for simplification of a tool that becomes increasingly complex.

Our discussion is divided into two sections. In the first (I) all arguments of which we are aware favoring the discard of subspecific names are listed, each supported in the initial paragraph under each topic by a brief explanation. A short commentary of one or more paragraphs follows each. In the second section (II) are listed a few other arguments, not readily incorporated elsewhere, in favor of the subspecies.

I

1. *Taxonomic recognition of one hypospecific grouping (geographic subspecies), and rejection of the other (gentes, strains, physiological subspecies, etc.) is inconsistent.* If trinominals are to be used at all there is no logical reason for restriction of their application to one particular type (the geographic subspecies) of hypospecies (Smith, *Turtox News, 33*:74–77) to the exclusion of others. Either all distinctive hypospecies should be recognized, or none. Since taxonomic recognition of grossly sympatric hypospecies is rarely practiced, the logical sequel is to discard any recognition of subspecies.

This is a strong point against acceptance of subspecies. Yet since we find we cannot consume all the cake, is it necessarily logical to reject it entirely? The door is not closed to general recognition of sympatric hypospecies (in fact some physiological "races" are accepted), and until it is, the progress in acceptance of geographic subspecies is scarcely to be discarded. Sympatric hypospecies merit nomenclatural recognition, although the proponent of names for them should realize that he bears a much more serious burden of proof than does the proponent of names for geographic subspecies. Even if practicalities do prevent nomenclatural recognition of sympatric hypospecies, the utility of the category "geographical subspecies" should not thereby be affected.

2. *Since virtually all subspecies as now recognized are geographic, one knows the subspecies involved if the locality is given.* Numerous faunal works, especially on vertebrates, have capitalized upon this principle in recent years. Subspecific names are omitted, or de-emphasized, ostensibly

to gain a simplicity that is presumed to be less repulsive to the tyro than the usual trinominal treatment. Actually the requirements even of the expert are thus satisfied, provided that care is used in handling geographic variation.

This is seemingly a strong point, but it is actually not as strong as it at first seems. True enough, locality alone can suffice for subspecific determination, but this is true only for organisms in which geographic variation is relatively well known. In most groups of animals, and in most areas of the world, locality alone is far from sufficient for subspecific determination. Not until geographic variation is fairly well known can locality provide a definite indication of subspecific identity.

Furthermore, acceptance of locality alone as the criterion for subspecific determination would exclude the possibility of taxonomic recognition of grossly sympatric hypospecies (gentes). If trinominals are to be regarded as unacceptable, they should not be rejected on the basis of being a mere substitute for locality; they reflect, or can reflect, niche as well as horizon or locality.

3. *Nomenclatural recognition of subspecies leads to acceptance of absurdly fine subdivisions identifiable only by locality or by study of large series of specific stages by experts.* The fine degree already attained by subspecific splitting in some vertebrates and parasites, whereby a different subspecies may be recognized from each valley, mountain, or host species, exemplifies the limit which splitting will eventually reach in all animals, if the temptation to name subspecies remains. Furthermore, there is no reason to suppose that the end has yet been reached even in the groups suffering from the finest taxonomic splitting. The absurdity of the trend is obvious. If the trend is not curbed, there is a real danger that taxonomy will become so topheavy as to topple and lose its utility.

Where differences exist, recognizable at any requisite taxonomic level, it is scarcely good science to refuse to recognize them. However, there is no reason to suppose that all animals are divisible into subspecies to the same extent. Quite to the contrary, animals may be expected to, and do, vary greatly in degree of taxonomic differentiation they exhibit. As a matter of fact, the degree of differentiation is of great evolutionary significance; that some population lines are plastic, others stable, is of fundamental importance.

The degree of difference required for a subspecies is, however, of great importance. The lower the requirement the more numerous will be the subspecies recognized, the greater will be the difficulty in defining them, and the more difficult will be determination of small samples. Certainly at least three-quarters of each population should be identifiable (the 75 percent-75 percent rule); in some groups more stringent requirements are generally accepted. Certainly a uniformity of practice is to be desired and no doubt will be forced into existence by sheer expediency. The present absence of uniformity does not of itself constitute a reasonable argument for abandonment of the whole rank of subspecies.

As generally defined, subspecies are recognizable entities. The fact that with increase in knowledge of characters and their variation subspecies should become recognizable only to experts is not to be lamented. The chief concern will be felt in groups in which amateurs have long been competent to recognize most of the forms recognizable even to the expert. In groups where amateurs have never ventured little or no chagrin is expressed over the fineness of distinction. The history of scientific study in every field discloses a succession of techniques permitting increasingly greater discrimination. The growth of taxonomy would be seriously stunted by cropping its most sensitive tendrils of discrimination.

4. *The formality of names for subspecies, even if subspecies are accepted, is unnecessary; symbols are equally useful and much simpler.* Even if the impor-

tance of defining and dealing with differentiated populations is admitted, naming of them, beyond the specific level, is a quite unnecessary, cumbersome custom. Symbols such as letters or numbers are much less cumbersome, and equally precise.

There can be no argument about the greater simplicity of numbers or letters over names. It is not a desirable simplicity, however, for the association of a name with a population should be memorized and retained much more easily than one with numbers or letters in place of a name. Names are not repeated with the frequency that letters or numbers would be in a series of related species. Furthermore, priority of symbol association would be necessary to avoid total confusion; the nomenclatural procedure applied to symbols would likely prove equally as formidable as that presently governing subspecific names, especially since it would necessarily be superimposed over at least certain parts of existing rules. Given that one must have labels of some sort for subspecies (and gentes), an established system of control of nomenclature should not carelessly be abandoned; the spectre of the confusion evident in anatomical nomenclature is a significant warning of what might be expected if controls on the labels for subspecies were abandoned. Use of symbols as a general policy does not appear practical.

5. *Elimination of subspecific names would greatly simplify nomenclatural procedure.* Certainly binominal nomenclature is simpler to govern by a set of rules than is trinominal nomenclature. The complexity of nomenclatural rules is immeasurably increased by the inclusion of subspecies within their scope.

The use of symbols instead of names for subspecies would not simplify matters (see preceding point). Furthermore, even if the subspecific rank itself—whether designated by symbol or name—could be disregarded completely, one type of complexity would still be substituted for another. What about names proposed in the past for subspecies that prove to be species? Would even a brief usage as a specific name of one originally proposed as a subspecific name have any bearing upon its availability? Or would it be better to disregard all subspecific names proposed after a given date? If so, would not all the complexities of new rules applicable after that date in effect simply be added to the complexities of rules governing names proposed before that date? If all names originally proposed for ranks less than the species are retroactively discarded, would not many changes ensue in specific names, particularly among vertebrates? This is not a proposal that works toward stability of names by any view.

6. *Disregard of subspecies or subspecific names will help to eliminate the base appeal of name-giving.* The number of subspecies probably exceeds the number of all other separate taxonomic entities together. Elimination of formal recognition of subspecies would remove over half the names in taxonomy. It is this vast reservoir of potential names yet to be proposed that appeals, basically, to many describers of subspecies. The appeal of name-giving (the *"mihi"* itch) does not merit the encouragement provided by formal recognition of its monstrous offspring. The danger of over-zealous splitting is likely to vanish with removal of the temptation to father, and be credited with, a name. Indeed, even if the subspecific rank must ultimately be generally admitted, use of symbols would obviate the appeal of sheer name-coinage.

It is perhaps astute psychological analysis that perceives the potential satisfaction to taxonomists of fathering a name assured of perpetuation. It is perhaps equally astute to perceive the possibility of base motivation through laziness for those who do not wish to recognize subspecies. If either is a prominent motivating force among taxonomists, then admittedly correctives are indicated. Neither accusation, is, of course, warranted as a generalization, although taxonomists

may be expected to exhibit on occasion the same frailties that beset other human beings. It is not, we believe, the name itself, nor its perpetuation, that appeals to taxonomists; it is the assurance of perpetual recognition of the geographic variation they have discovered that appeals to them. The desire that the facts discovered in approved research procedures be not disregarded is not base, and certainly the formal recognition afforded by the application of a customarily acceptable name provides the desired assurance. The name itself is, I believe, of little significance relative to the entity segregated. Symbols could never provide the assurance names do that future workers must at least consider the validity of the geographic variability presumably discerned.

It is true that symbols would categorically eliminate any possible appeal of sheer name-coinage, but they are impractical (see No. 4) except in special situations.

7. *The subspecies is inconsistent with all other nomenclatural ranks in not requiring reproductive isolation or an equivalent thereof.* Species are generally agreed to be reproductively isolated Mendelian populations. Great emphasis has been placed upon the requirement for reproductive isolation as that is the basic requirement to distinguish the specific from the subspecific rank (the latter not possessing reproductive isolation or the equivalent thereof). All higher categories require reproductive isolation, as do species. This inconsistency between subspecies and all other taxonomic categories collectively, may be regarded as providing good reason for elimination of the offending inconsistency.

The inconsistency certainly exists, but the given deduction may be admitted as valid only if the basic function of nomenclature is agreed to be the expression of the relationship of populations throughout all ranks of classification. This is not the case. The primary function of nomenclature at the generic, or lower, level is to provide labels for recognizably different populations. Clearly single names or symbols are not adequate for this purpose; two or three are used (generic, specific, subspecific names). The use of two or more words has a *grouping* function, showing relationships, even at the generic level. Above the generic level the hierarchy of nomenclature serves primarily to indicate degree of relationship. On the other hand relationship reflects difference. As a matter of fact, fundamentally it is *difference* that nomenclature in general must show, since the basic blocks (species, subspecies) themselves are based upon differences. The criteria for the subspecific rank are thus wholly consistent with the fundamental theory of nomenclature. True enough, the species might be recognized as the lowest recognized level of difference, but the fact remains that conspicuously different populations exist that do not happen to be as unrelated to each other (i.e., as reproductively isolated) as the species definition demands. Furthermore, it is a commonplace that many subspecies are more different from each other than are many species (especially sibling species), and that it is not degree of difference that differentiates species from subspecies, but reproductive isolation. The shoe fits the other foot: inconsistency with the basic aim of nomenclature applies to species, not subspecies, for the limiting factor is but remotely related to the common feature (difference) in classification. In the end, all nomenclatural ranks have equally arbitrary and vague limits, both upper and lower, except for the species, which has a theoretically objective lower limit. The subspecies is not exceptional. Any rank of nomenclature may be regarded as vulnerable to attempts at simplification or elimination. Any one rank probably could be eliminated without insuperable loss.

8. *The ostensible differences between subspecies more often than not are selected arbitrarily and with admitted bias favoring the desired split.* Students of geographic variation are beginning to realize that most, if not all, recognized

subspecies differ in more than one character, and that commonly either (a) the area of intergradation between the extremes of one character is quite independent of the area of intergradation in another character (this may be designated as *staggered intergradation* as opposed to *coincident intergradation*), or (b) the extremes blend clinally, or (c) only one sex or age group (or both!) exhibit differences. Characters are now seen to exist as entities in themselves, each interacting with the environment in its own peculiar way, and thus coincidence in a single area of intergradation in two or more characters is the unusual rather than the expected occurrence. If the interests of unbiased truth are to be served in taxonomy the deliberate selection of desired data so characteristic of subspecific delimitation is not to be condoned. Certainly the recognition of subspecies whose ranges are exceeded, even greatly exceeded, by a supposed area of intergradation is anomalous and a travesty upon objectivity.

The situation is not wholly as indicated. The purpose of taxonomy is to delimit differing populations, and if populations differ only in one sex or at one ontogenetic stage then they can be defined only on the basis of that sex or stage. This means that only a part of a random sample will be useful in the determination of the identity of a population, but this does not detract from the existence of a real difference between populations. The taxonomic subspecies is presumably based upon genetic differences; that the genetic differences may be expressed phenotypically in only one sex or ontogenetic stage does not alter the validity of belief in the existence of genetic differences. The genetic differences must only be such that they produce a phenotypically recognizable difference of a given degree (75 percent, 95 percent, 98 percent) in individuals in which the genotype can be expressed. To require the genotype to be expressed in stages or a sex in which it cannot be expressed is illogical.

Furthermore, both staggered and clinal intergradation are to be expected in primary intergradation, much less frequently in secondary intergradation. Perhaps, as discussed below, recognition of populations united by certain types of primary intergradation should be withdrawn; debate on this question still continues. Populations united by other types of primary intergradation on the other hand, certainly do merit recognition, as generally do those united by secondary intergradation.

9. *The subspecies is not an actual entity in nature, and therefore nomenclatural recognition is spurious.* As generally conceived by their proponents, hypospecies are regarded as actualities that are usefully recognizable in zoological nomenclature. The whole defense of subspecies necessarily hinges upon this premise, but the premise is vulnerable insofar as subspecies are taken to be actualities. Organisms do become adapted to different environmental conditions. Groups of them acquire unique combinations of limits of tolerance to degrees of fluctuation in environmental factors. The limits may become narrower through increased sensitivity, or broader through decreased sensitivity. Organisms thus rather reliably reflect their environment. Where reproductive compatibility is not involved, any observed differentiation is, in reality, a graphic record of environmental variation. Taxonomic recognition of hypospecies is, then, the recognition of the existence of a given combination of environmental conditions to which a group of organisms of one species has become adapted. Since an infinite number of environmental factors exist, an infinite number of adaptive types may evolve, and the more improved the techniques of study, the more of these adaptive types will become evident. Classification of reproductively compatible organisms thus becomes a classification of combinations of environmental factors to which adaptation has been made. This is not the objective of zoological taxonomy.

It is true that subspecies are creatures

of their environment, but only in part. They are functions (mathematically speaking) of their environment *and* their genetic composition, responding to a given shift of environment only as their own particular and peculiar genetic makeup permits. In a way one may view any given population as a product of its reactions to environments *past and present*. Population *A*, which has remained hundreds of thousands of years in a given environmental situation, responds differently to it than does one of its segments *B*, which has invaded other climes during that time and ultimately returned to the original habitat. *B* bears the indelible genetic imprint of its constant adjustment to changing environments. The many known cases of overlap by the terminal members of circular chains of subspecies illustrate conclusively that hypospecies are more than functions of the environment alone. Were they but functions of the environment, they would have no claim to reality, as something apart from the environment; but as products of both environment and heredity they may reasonably be considered as something distinct—as an actuality.

The subspecies that unquestionably differ in history (genetic background) thus may qualify for recognition, provided, of course, that the proper level of difference exists. Most, if not all, subspecies that are united by areas of secondary intergradation would be included. Some geographically disjunct (allopatric) subspecies would be included, others not, but because of the impracticality of determining details of history the proper level of difference will be the sole criterion of acceptance or rejection for such populations.

However, any two subspecies united by areas of primary intergradation pose serious problems. Such subspecies are segments of a population in the process of subdivision, and thus have a common genetic background; they have not acquired genetic differences through periods of evolution apart from each other. The areas of intergradation in such situations may be expected to correspond with regions of environmental shift, whereas they do not necessarily do so in cases of secondary intergradation. In some areas, with sharply defined physiographic features, the zones of environmental shift unquestionably are narrow and largely coincident; in other areas, of more gently transitional topography, the zones of environmental shift are broad and tend to be more staggered, less coincident. These differences are naturally reflected in the organisms. Subspecies in regions of rugged topography tend to have sharply delimited ranges; those of essentially flat areas tend to be connected by broad and/or staggered zones of intergradation. In those species having staggered adaptive responses, recognition of subspecies does not appear logically tenable unless the number of coincident character-shifts actually exceeds the number of staggered-character shifts. The practice of summation of character differences in order to achieve the proper level of difference should be countenanced only for truly coincident characters. Infraspecific populations apparently differing in but a single character may be assumed to have other intangible differences correlated with the mensurable character and should be evaluated accordingly.

Sympatric hypospecies are comparable to the subspecies of regions of rugged physiography, not to those of uniform topography. The ecological zones that do exist sympatrically, where hypospecies may differentiate, provide adaptive zones as extensively different from each other as the extremes in any zone compared at both high and low altitude. Differentiation in sympatric ecological zones (as hypospecies), like differentiation in allopatric regions of rugged physiography (as geographic subspecies), tends preponderantly to involve coincidental rather than staggered environmental shifts.

II

Several arguments unrelated to the preceding discussion may be presented in favor of the subspecies.

1. *Subspecific names are optional.* Several objections to subspecific names have been raised on the grounds that the names are superfluous, introduce needless complexity or add nothing important that symbols or statement of locality could not give. Most of these objections can be avoided, where valid, by the simple device of omitting the offending names. Subspecific names are not essential to a scientific name, and where they are needlessly burdensome they can and should be dropped. This does not mean they should be disregarded in all circumstances, for generally they serve useful ends despite their drawbacks.

2. *Inferential nature of most species renders the names applied to objectively determinable subspecies more stable than specific names alone.* In very few cases has it been possible to determine whether or not related allopatric or parapatric populations are reproductively isolated. Degree of morphological overlap has been taken as the best indicator, but this has proved unreliable in many cases, for sympatric sibling species are often virtually indistinguishable, allopatric subspecies much more widely different in visible characteristics. Thus, with good reason authors may differ in opinion as to whether a given population should have specific or subspecific status. In all except the nominate subspecies of a polytypic species, the species name for a given population will vary according to the opinion of rank held by the author.

Suppose, for example, five forms, *A–E,* are named at 10 year intervals, respectively, from 1910 to 1950. If all are taken as species, each will bear its specific name of *A, B, C, D,* or *E.* If *D* and *E* are regarded as belonging to (subspecies of) one species, then *E* will bear the specific name *D.* If *C, D* and *E* are regarded as species of one species, then *E* would be known by the specific name *C.* It can be seen that any one of five specific names could be used for population *E.* If that population occurred in one state, say Arizona, accounts of the fauna of that state then might refer to the same form (*E*) under five different names, not reflecting in any way that they apply to the same form. If the subspecies is used, the name *E* will be present and provide stability of communication no matter what species name might be appropriate. Only where specific or subspecific rank is well fixed is it feasible to eliminate the subspecific name without danger of loss of clarity. This sort of predicament cannot be dismissed as occurring with inconsequential frequency. Since species status is so often not determinable (despite the objectivity of its qualitative criterion), the much more objectively determinable subspecies (despite the subjectivity of its quantitative criterion) is far more practical in many cases.

3. *Disregard of the subspecies will place undesirable emphasis upon a frequently indeterminate relationship—upon guesswork instead of determinate objectivity.* If subspecific names are not to be recognized in new taxonomic work, at least the more distinct parapatric and allopatric populations will more frequently than now be given specific instead of subspecific names. In most instances specialists now lean over backward to designate a new form as a subspecies, chiefly because a subspecies shows relationship in a way which a species does not, and partly because this has come to be accepted as the most desirable, conservative policy. Any reasonable excuse is now seized to call a form a subspecies. If the subspecies is eliminated, any reasonable excuse will be seized to call a form a species, and defensibly so. It is not necessarily a "base" instinct that would motivate this shift of emphasis.

On the other hand, the less distinct parapatric and allopatric populations will rarely be named, whereas in fact they may often merit names. In either case, a most unfortunate premium would be placed upon guesswork on the part of the taxonomist relative to the rank of a given form; indeed the status of allopatric and parapatric forms is usually a matter of an

educated guess. At the present time, with emphasis upon the more objectively determinable subspecies, the inferential bases for assumption of specific status are not of serious consequence.

4. *Recognition of the subspecies is an aid to the understanding of evolution.* Certainly the most important hypospecific rank is the subspecies, through which stage many, if not most species have passed. The gap from non-species to recognizable species is necessarily bridged by stages of major evolutionary import. The recognition of potentiality for speciation in intermediate populations has become a major part of taxonomy. When the word "subspecies" is used, it is meant to imply that according to the judgment of the taxonomist the population has attained such a degree of recognizable differentiation as clearly to demonstrate the potentiality for speciation. It is not implied that all subspecies are destined to become full species. Indeed, the potentiality of reversal of the trend toward differentiation is as important an evolutionary concept as attainment of the specific level. The subspecies concept has thus contributed materially in the past to an understanding of the manner in which at least some species have evolved. It will be of continued importance in the future.

Admittedly the subspecies concept has also been of undesirable influence in the growth of evolutionary thought, through fixation for a considerable time of the belief that all species evolved from subspecies, and that subspecies were *ipso facto* incipient species. Recent thought reveals that any given subspecies is a link between non-species and species by fortuitous occasion only. That it may be a link at all, and apparently such an important link, adds further reason for retention of that rank.

Conclusions

The desirability of taxonomic recognition of hypospecies (including subspecies) hinges upon (*a*) the soundness of the hypospecies as an entity, (*b*) the justifiability of recognition of individual hypospecies, and (*c*) the generality of agreement upon minimum requirements for nomenclatural recognition (granting that *all* taxonomic categories are defined arbitrarily). Reality (or soundness) of the hypospecies entity seems assured; the subspecies is a real, natural stage in evolution of Mendelian populations. For many reasons, centering about both distinctness and evolutionary role, subspecies are justifiably recognized. Agreement upon minimum requirements is within the realm of practicality, but requires careful consideration of borderline zones.

We suggest that effort be focussed on (1) common acceptance of a certain minimum degree of difference (in excess of 70 percent), (2) rejection as hypospecies of infraspecific aggregations based on characters correlated with staggered and/or clinal environmental features, and (3) admission of sympatric hypospecies for nomenclatural recognition by trinomen when proof of merit is adequate.

We believe that the basic mechanism utilized in the past to maintain nomenclatural stability and clarity merits retention, although actual use of the trinomen may be regarded as optional.

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What Is Species Describing?

Perhaps no statement in the language of the systematist is subject to as much misinterpretation as the common, "I am going to describe a species." In his interesting recent article, "Species and Systematics" (*Syst. Zool., 5,* 1–10), R. B. Clark shows that even an expert systematist can become trapped in this pitfall when he deplores "that descriptions of species are still based, at least theoretically, on descriptions of single type specimens."

It is indeed true, especially in entomology wherein there are so many species to describe, that often the only contribution toward the description of a species *is* the description of a single type specimen. But if time, publication space, or a limited number of specimens permits only one description to be made, I am sure that most systematists would prefer that this be a representation of the holotype rather than a composite description of a series of specimens representing the author's concept of the species.

The validity of such a preference is clear when one considers that the verbal description serves merely as a substitute for, or a supplement to, an illustration of the object or the opportunity for examining it personally. One would not accept a composite illustration or a composite specimen as a sound reference tool, why accept a composite word picture?

The confusion in the use of the term "species description" is between the fixation of a species name to a single type specimen, on the one hand, and the endless task of actually describing a species, on the other. The fixation of a species name to a specimen, however arbitrary such action might be, is one of the most useful and least subjective, of the taxonomic procedures. It is the closest approach toward making systematics an "exact science." The description immediately following the new name should be an effort to let other workers know the *nature of the holotype,* it is not the occasion to make known the *nature of the species.* Needless to say, the description and illustrations of the holotype should not include details of other specimens unless these inclusions are clearly indicated as such.

Once the new species name has been proposed and affixed to a single, described specimen from a precisely stated geographic locality and, if possible, a known ecological niche, then the real business of species describing can begin. This is potentially an endless job, for such descriptions should, in theory, eventually include everything we can learn about a species. I need only cite *Homo sapiens* L. as an extreme example of all the intricate contributions which can be made to the description or knowledge of a species. Such a broad concept can be dynamic and thus take into account the steady changes that species and their races undergo in the course of time. With this in mind we can, for example, keep the description of the housefly up to date as at least its physiological nature is changed by the selective effect of such factors as DDT in the environment.

The fixation of a new species name to a single decribed specimen is thus merely a legal action, but one which inevitably makes a contribution toward a species description. Depending on the extent of his sample of specimens, and his biological data, the proposer of a new name can often in the same paper contribute much more toward a fuller species description. Such information as knowledge of secondary sexual characters, analysis of population samples, variation, geographic distribution, life-history stages, and biology are among the many contributions which can be made at the time a new species name is proposed.

Incidentally, if the above reasoning is valid, I believe it follows that paratypes, to have real worth, should reflect the *nature of the holotype* and not the author's *concept of the species.* The author's dated

identification labels are sufficient for the latter purpose. Thus, not all conspecific specimens before the worker should become paratypes. Those that do must not only be from the type population and of the same sex but also must be arbitrarily selected so as to match the holotype as nearly as possible. Such specimens when distributed to appropriate research centers can truly serve as the next best thing to actual possession of the holotype. All other specimens before the author, including perhaps allotypic specimens (which, obviously, cannot exhibit all of the holotype's characters), can be treated as "other specimens examined." One may argue that, because paratypes have no nomenclatorial status or recognition, they need not be selected with such precision. The fact remains, however, that paratypes are constantly being designated. This is a plea for elevating their prestige and value as reference material.

Well-described, preserved holotypes are thus the anchor points of taxonomy. They are important not only at the species level but also in fixing, at least theoretically, the names of all higher categories. Their importance is best realized by systematists who are attempting to classify a little-studied, inadequately sampled, taxonomic group. To such pioneers holotypes can be compared to trail blazes in a tangled, unexplored (or poorly explored) forest. The blazes do not describe each section of the forest, nor do they indicate where one is going, but they are vital in charting the path and in guiding others wishing to retrace it. Indeed, they can even help prevent an undesirable duplication of effort. Once the "taxonomic forest" is well explored and "mapped," old blazes (the types) are used less and less and finally become merely of historical interest. This, I dare say, is the status of many holotypes in such fields as ornithology.

Systematists in different fields of biology work at different levels of knowledge. It is to be hoped that those confined to well-trodden territory, who have never had to face the uncertainties and gropings of a pioneer, will at least try to appreciate the explorer's problems and methods of meeting them.

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The Division of Biological and Medical Sciences of the National Science Foundation announces that the next closing date for receipt of research proposals in the life sciences is May 15, 1957. Proposals received prior to that date will be reviewed at the Summer meetings of the Foundation's advisory panels, and disposition will be made approximately four months following the closing date. Subsequent closing dates will be September 15, 1957, and January 15, 1958. Inquiries should be addressed to the National Science Foundation, Washington 25, D. C.

The Museum of Comparative Zoology at Harvard College has recently added to its staff Dr. Herbert W. Levi, new Assistant Curator in charge of Arachnida. Dr. P. J. Darlington, Jr., Curator of Insects, has completed his major work on zoogeography, and this is expected to reach publication in book form during the summer of 1957. Dr. Darlington has begun a research tour of eastern Australia as a Guggenheim Fellow, and is expected to be away from the Museum until 1958.

SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Consult recent issues for the style to be followed in the preparation of manuscripts. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.

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